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PUSA

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OF THE

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ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

1. Coat Colour in Greyhounds.

By ADAIR DIGHTON, F.R.C.S., F.Z.S.

[Animal Breeding Research Department, University
of Edinburgh.]

[Received October 13, 1922 : Read February 6, 1923.]

Some months ago, my friend Mr. J. R. Robertson, knowing that I was interested in both the problems of Heredity and in Greyhounds, suggested that I should make extractions of their various coat colours from the stud books, and tabulate them on a definite plan with a view to ascertaining whether the results accorded with Mendelian principles and with previous data obtained by him from direct experiment. At the time Mr. Robertson suggested this, I was too busy with other affairs to undertake it, but at the end of the last coursing season I began what has been a hard but fascinatingly interesting work.

By way of preface, I should explain that the National Coursing Club is the ruling body in the coursing world, and under its direction the Greyhound Stud Book is issued annually. A rule of the Club stipulates that every litter of greyhounds must be registered within two months of the date of whelping, with the names of the sire and dam, and the colour (subject to correction within six months of the date of whelping), sex, and number of the puppies. In this way there is in the Greyhound Stud Book of the present day an authentic record of every greyhound born.

From the point of view of accuracy in the present statistics it is unfortunate that colour registration should have to be made at so early an age, for there is no doubt that in many cases colour changes with age, and there may be, in fact are, cases in which the colour would have been registered differently had the date of registration been postponed. There is one other point to which I would draw your attention. Under the heading of "Registration Regulations" there is the following instruction:—

"It is not desirable to register a colour which is not seen by the judge when following the dogs. Thus it often happens that a black dog has an insignificant patch of white on his chest, it may be a few white hairs on the tip of his tail or a white toe. The entry of such a dog as black and white simply leads to confusion, and should be avoided."

From the practical standpoint this is an excellent rule, but it is not conducive to that accuracy in description which is of such vital importance when dealing with colour from a scientific or statistical point of view.

Bearing these points in mind. I began with the Greyhound Stud Book for the year 1907, and have worked through the fifteen succeeding volumes up to, and including, that published in 1921. In this way the records of 16,260 litters have been examined and the colours of 25,767 whelps have been tabulated. The pigmentary factors of greyhounds resemble those of other animals in that they consist of black, chocolate (known as red), and yellow. In addition, the greyhound has a composite colour known as brindle, which is due to a pattern factor combining with one, or more, of the other colours. The results, generally, may be taken to represent the actual colours of the various individuals, but personal observation shows that there are certain discrepancies. Thus there are blacks, so registered, that show brindle markings, and the returns do not differentiate, in the majority of cases, between red and fawn, the usual description being "red or fawn," which explains why it has been necessary for me to group these two colours together under one heading. Pure albinism of the skin and hair is very rare, but partial albinism is common in the pied patterns. Other colours, or combinations of colours, such as blue-brindle, blue-fawn, black-brindle, etc., are often met with, but these are too ambiguous to be taken into account and are not included in my figures.

Take first the matings of black to black. On the assumption that black and blue are dominant over all other coat colours, the blacks can be of two kinds: pure dominant blacks, containing nothing but black factors, and impure dominant blacks, containing one black factor and one alternative factor, which may be either brindle, or red, or fawn. Now, though pure dominants do occur in all colours, they are rare. Greyhounds are bred for speed and work. Colour is a minor consideration, and of the thousands of dogs born, only a very small percentage of them

ever stand at stud, and, of these, only very few have a sufficient number of mates upon which an assumption of pure dominance could be based. For these reasons it may be taken that the parents concerned in the 500 black to black matings were impure dominants in genetic composition. The 500 matings yielded 3603 whelps, and, on the basis of the classical Mendelian ratio of 3:1, the expectation is that there would be 2700 blacks to 900 brindles, red or fawns, and whites. The observed results gave 2697 blacks and blues to 906 brindles, red or fawns, and whites.

In the black to blue matings, of which there were 231, there were 1338 whelps, and the expectation is the same as in the black to black matings: namely, three blacks and blues to one other colour. This would give 1003 blacks and blues to 335 brindles, red or fawns, and whites. The actual results were 998 to 340.

These figures clearly establish the premise that black is the epistatic colour, and is dominant over all others.

Take next the matings of black to brindle. The case here is one of an impure dominant to a recessive, so that the resulting offspring should be an equal number of impure dominants and of recessives. That is to say, there should be an equal number of blacks and blues to brindles, red or fawns, and whites. The number of whelps in the 500 matings was 3053, so that there should have been 1526 of each. The actual result was 1533 blacks and blues to 1520 brindles, red or fawns, and whites.

In the black to red or fawn matings the case is again one of impure dominant to recessive. Again equality would be expected, so that of 3039 whelps there should be 1519 of each. The actual result was 1525:1514.

These figures still further conclusively prove that black is epistatic to brindle and to red or fawn.

Take now the blue matings. I have taken up the black to blues. In the blue to brindle matings the case is one of impure dominant to recessive, and the expected result from 1293 whelps would, therefore, be 646 blacks and blues to 646 brindle, red or fawns, and whites. The actual result was 649:644.

Blue and red or fawn matings fall into the same scheme, and from 1822 whelps the result should have been 911:911, whereas it was actually 915:907.

The blue to blue matings only numbered 25, and resulted in 132 whelps. Here the scheme is impure dominant to impure dominant, which should give 3 blues and blacks to 1 brindle, red or fawn, and white. The expected result was therefore 99 blues and blacks to 33 brindles, red or fawns, and whites. The observed result was 93 to 39.

In the table it will be seen that in these matings there were 6 blacks and 1 black and white, and this, or these, raise a difficulty. Blue is undoubtedly a dilute black, and the previous small incidence of blues clearly shows that if there is a special

dilution factor, it cannot be epistatic to the saturation factor. In these circumstances it must be recessive, and being so, there should be no blacks in the blue to blue matings. Very possibly the blacks were dark blues verging on black, but, anyhow, the blue to blue matings are too few to form a reliable guide.

Turning next to the brindle and brindle matings. On the hypothesis that brindle is recessive to black and blue and dominant over red or fawn and white, there should be no blacks or blues from brindle to brindle matings. Theoretically, with the blackness stripped off, the brindles become dominant or, as dominants are rare, impure dominant to the recessive red or fawns and whites. Thus the mating is one of impure dominant to impure dominant, and the expected result from 2829 whelps would be 2121 brindle to 707 red or fawns and whites. The actual result was 30 blacks and blues: 2118 brindles and 681 red or fawns and whites.

The 30 blacks were made up of 14 blacks; 9 black and whites; 6 blues and 1 blue and white. The error of deviation is so small that I think it may be laid down to inaccuracy of description.

In the case of brindle to red or fawn, there were 2932 whelps, and as it was a case of impure dominant to recessive the expectation was that there would be equality or 1466 brindles to 1466 red or fawns and whites. The actual result was 1465 to 1458, but there were, in addition, 9 blacks, which once again, though unsatisfactory, must be attributed to descriptive error.

The last of the more simple results are reached in the matings between red or fawn and red or fawn. On the hypothesis that red or fawn are hypostatic to everything but white, the expectation is that there would be no colours in the 2925 whelps but red or fawns and a few whites. Actually, the figures observed were 10 blacks, blues and brindles: 2910 red or fawns and 5 whites. The incidence of the epistatic colours black, blue, and brindle is so low that one is justified in assuming that their presence in this mating is due to personal error rather than to genetics.

Reviewing the above results, I think I have proved that greyhound coat colours follow the sequence of black, which is epistatic, blue, brindle, red or fawn, and white, which is hypostatic, and that, secondly, blue is a dilute black.

From supplementary statistics I find that there are undoubtedly pure dominants for both black and brindle, and, as I have shown, red or fawns breed true, which is invariably the case with a recessive character. Thus it follows that if such were of any practical use to the coursing man, he would have no difficulty in establishing pure breeding strains of either black, brindle, red or fawn.

I now turn to the secondary results of the matings, and these are somewhat more complicated than the primary data already discussed.

In the black to black matings, if the blacks are taken as impure dominants and of two sorts:

- (1) blacks carrying a brindle factor as recessive,
- (2) blacks carrying a red or fawn factor as recessive,

and the incidence of both blacks are equally numerous, the ratio arising should be:—black, 12 : brindle, 3 : red or fawn, 1. Further, if every black dog or bitch carried both brindle and red or fawn factors, the incidence would be the same, as red or fawn could only appear in the absence of brindle.

It will be observed that the incidence of black came out correctly in the black to black and blue to blue matings, but in the place of the brindles being in the ratio of three to one red or fawns, the colours are almost equally distributed in the black to black matings, whereas in the blue to blue matings the red or fawns are almost twice as numerous as the brindles. These results cannot be explained by the law of probability, based on the interaction of factors arising out of the hypothesis, already proved, that brindle is dominant over red or fawn.

In the mating of black to brindle, the Mendelian expectation is:—black, 4 : brindle 3, red or fawn 1; and the 3053 whelps should therefore give 1526 blacks : 1145 brindles and 381 red or fawns and whites. The observed results gave 1533 blacks and blues: 1018 brindles and 484 red or fawns and whites.

Here the results are sufficiently close—having regard to the fact that the actual incidence of the recessive factors in the DR blacks is unknown—to be taken as in accordance with probability.

On the other hand, the Stud Book returns for black to red or fawn show, as regards the incidence of brindles and red or fawn, a totally unexpected result. In the 3039 whelps the expected result was that there would be 1519 blacks: 789.5 brindles and 789.5 red or fawns; whereas the actual result was 1525 blacks: 492 brindles, and 1007 red or fawn and whites. At the moment the explanation of these figures is beyond me, but I think it is worth noting that in the black to black matings the incidence of brindles and red or fawns is practically equal, and the same holds true in the black to blue matings. In the black to brindle and the black to red or fawn matings there is again a similarity, as in the former the ratio of brindle to red or fawn is as 2 to 1, whilst in the latter the ratio is practically reversed. This may be nothing more than a coincidence of figures, but somehow I think it holds the key to the explanation. My own idea was that black carries a factor which produces either brindle or red according as to the factor introduced by the other parent, but if this were so, in the black to red or fawn matings there should be no brindles, whereas there were actually 492 in 3039 whelps.

In passing to the mixed colours, it is interesting to note that

throughout the series the mixed combinations very generally follow the same incidence of ratio as the whole colours with which they are associated.

Let me now devote a few words to the mixed matings—that is to say, the “pied” colours, in which white plays a leading part on both sides. These unions, on the whole, fall into line with those of melanistic character. One would have expected a higher incidence of whites in these matings, but it is interesting and important to note that in the red or fawn and white to red and fawn and white, the hypostatic colours in the scale, there are more whites than in any other matings. It seems probable that the mixed colours tend to segregate into the conditions of melanism and albinism of the skin and hair, giving 1 whole colour : 2 mixed colours : 1 white. When we recall the instruction concerning the registration of colours, it is self-evident that there is a very appreciable chance that some mixed colours are nearly white. This being so, there should be about 3 “mixed” to 1 whole colour in the pied matings.

Adding the “white” to the “pied” in the whole series, it will be found that the total is 2413 “pied” and white to 689 whole colours, which gives a ratio of 3·5 to 1, which is sufficiently close for all practical purposes.

In conclusion, I must thank Mr. Robertson for all the help he has given me in drawing up this paper and Mr. Martin Duncan, our Librarian, for his kindness in furnishing me with what references on the subject there are.

WHOLE COLOUR MATINGS.

BLACK × BLACK.

Matings. 500.

Whelps. 3803.

Bk. 1607	Be. 196	Bd. 314	R. or F. 271	W. 21
BkW. 796	BeW. 98	BdW. 162	R. or FW. 138	
2403	294	476	409	21
2697			906	
<i>Expectation.</i>	2700		900	

BLACK × BLUE.

Matings. 231.

Whelps. 1338.

Bk. 616	Be. 226	Bd. 112	R or F. 162	W. 7
BkW. 118	BeW. 38	BdW. 32	R or FW. 27	
734	264	144	189	7
998			340	
<i>Expectation.</i>	1003·5		334	

BLACK X BRINDLE.

Matings. 500.

Whelps. 3053.

Bk. 1115	Be. 123	Bd. 869	R. or F. 395	W. 18
BkW. 258	BeW. 37	BdW. 149	It. or FW. 89	
1373	180	1018	484	18
1533			1520	
<i>Expectation.</i>	1526		1526	

BLACK X RED or FAWN.

Matings. 500.

Whelps. 3039.

Bk. 1130	Be. 146	Bd. 400	R. or F. 877	W. 15
BkW. 223	BeW. 17	BdW. 92	R. or FW. 130	
1362	163	492	1007	16
1525			1514	
<i>Expectation.</i>	1519		1519	

BLUE X BLUE.

Matings. 25.

Whelps. 132.

Bk. 6	Be. 76	Bd. 12	R. or F. 23	W. —
BkW. 1	BeW. 10	BdW. 1	R. or FW. 3	
7	86	13	26	
93			39	
<i>Expectation.</i>	99		99	

BLUE X BRINDLE.

Matings. 213.

Whelps. 1293.

Bk. 369	Be. 175	Bd. 349	R. or F. 189	W. 2
BkW. 73	BeW. 32	BdW. 74	R. or FW. 30	
442	207	423	219	2
649			644	
<i>Expectation.</i>	646		646	

BLUE X RED or FAWN.

Matings. 291.

Whelps. 1622.

Bk. 519	Be. 249	Bd. 164	R. or F. 598	W. 6
BkW. 116	BeW. 31	BdW. 60	R. or FW. 89	
635	280	214	667	6
915			907	
<i>Expectation.</i>	911		911	

BRINDLE X BRINDLE.

Matings. 500.

Whelps. 2829.

Bk.	14	Be.	6	Bd.	1898	R. or F.	527	W.	18
BkW.	9	BeW.	1	BdW.	220	R. or FW.	139		
	23		7		2118		663		18
			30		2118				681
<i>Expectation.</i>			0		2121				707

BRINDLE X RED or FAWN.

Matings. 500.

Whelps. 2932.

Bk.	9	Be.	—	Bd.	1343	R. or F.	1287	W.	4
BkW.	—	BeW.	—	BdW.	122	R. or FW.	167		
	9		—		1465		1454		4
			9		1465				1458
<i>Expectation.</i>			0		1466				1466

RED or FAWN X RED or FAWN.

Matings. 500.

Whelps. 2925.

Bk.	2	Be.	2	Bd.	1	R. or F.	2540	W.	5
BkW.	4	BeW.	1	BdW.	—	R. or FW.	350		
	6		3		1		2910		5
			10				2910		5
<i>Expectation.</i>			0				2920		5

MIXED COLOUR MATINGS.

BLACK and WHITE X BLACK and WHITE.

Matings. 100.

Whelps. 532.

Bk.	92	Be.	16	Bd.	24	R. or F.	32	W.	4
BkW.	280	BeW.	12	BdW.	56	R. or FW.	16		
	372		28		80		48		4
			400				132		
<i>Expectation.</i>			399				133		

BLACK and WHITE X BRINDLE and WHITE.

Matings. 100.

Whelps. 552.

Bk.	48	Be.	16	Bd.	64	R. or F.	44	W.	4
BkW.	176	BeW.	32	BdW.	116	R. or FW.	52		
	224		48		180		96		4
			272				280		
<i>Expectation.</i>			276				276		

BLACK and WHITE × RED or FAWN and WHITE.

Matings. 100.

Whelps. 564.

Bk.	72	Be.	10	Bd.	22	R. or F.	52	W.	22
BkW.	184	BeW.	14	BdW.	78	R. or FW.	110		
256		24		100		162		22	
		280				284			
<i>Expectation.</i>		282				282			

BLUE and WHITE MATINGS too few to be used.**BRINDLE and WHITE × BRINDLE and WHITE.**

Matings. 100.

Whelps. 430.

Bk.	—	Be.	—	Bd.	50	R. or F.	34	W.	5
BkW.	—	BeW.	—	BdW.	270	R. or FW.	71		
—		—		320		105		5	
				320		110			
<i>Expectation.</i>				321		107			

BRINDLE and WHITE × RED or FAWN and WHITE.

Matings. 100.

Whelps. 502.

Bk.	8	Be.	8	Bd.	32	R. or F.	68	W.	20
BkW.	14	BeW.	4	BdW.	220	R. or FW.	123		
22		12		252		196		20	
				252		216			
<i>Expectation.</i>		0		251		251			

RED or FAWN and WHITE × RED or FAWN and WHITE.

Matings. 100.

Whelps. 631.

Bk.	—	Be.	—	Bd.	—	R. or F.	53	W.	62
BkW.	—	BeW.	1	BdW.	2	R. or FW.	513		
—		1		2		566		62	
<i>Expectation.</i>		0		0		569		62	

2. A Note on the Zoæa of a Land-Crab, *Cardisoma armatum*.

By H. GRAHAM CANNON, B.A., F.Z.S.

[Received October 24, 1922 : Read March 6, 1923.]

(Text-figures 1-6.)

Among the Land-Crabs it is known that the females of the genera *Gecarcoidea* and *Gecarcinus* resort to the sea in order that the young aquatic larvæ, on hatching from the eggs, may swim away into the water. According to Moreira [1912] ripe females of *Cardisoma guanhumi* also resort to salt or brackish water for this purpose, whereas, according to Calman [1909], neither Ortmann nor Andrews observed any specimens of the *Cardisoma hirtipes* in the neighbourhood of the sea.

During September 1922 a female land-crab of the species *C. armatum* Herklots, kept in captivity in the Society's Gardens, was noticed to be carrying a large mass of eggs underneath the abdomen. The eggs proved, on examination, to be fertile, and in a late stage of development. It was obviously of interest to find out whether the eggs of this species would hatch in fresh or in salt water.

Some eggs were removed from the female and placed in pure artificial sea-water, while others were placed in tap-water. A third lot were put into brackish water made of equal parts of sea-water and tap-water. The next day all the eggs appeared healthy, and the embryos in most showed a fairly regular heart-beat. After two days those eggs in the tap-water had become opaque, more especially in the central part of the egg, while those in brackish water and sea-water appeared to be developing normally. After three days many of the sea-water eggs hatched out and the young appeared quite vigorous. In the brackish water only a few hatched out, but these also appeared quite healthy. In the fresh water some of the eggs had burst the shell, but the young had disintegrated. It appears very probable from this that *C. armatum* also resorts to the sea, or at least to brackish water for spawning-purposes.

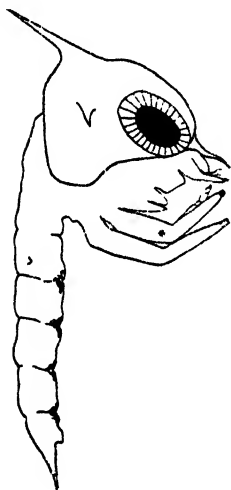
The larvæ only survived a few days after hatching and did not develop further, although they were being offered the diatom *Nitzschia* as food. It could not be seen whether the larvæ were actually taking the diatoms into their stomachs.

The larvæ were typical Brachyuran zoææ. The frontal spine slopes downwards and then curves upwards, and ends by re-curving down again (text-fig. 1). There is a pair of lateral spines projecting outwards and slightly forwards (text-fig. 2). All the spines of the carapace are simple. The antennæ are very simple

(text-figs. 3 & 4) and the second antenna does not bear a lateral spinous process (text-fig. 4). The 1st abdominal segment bears at each side a short forwardly directed spine, the other segments being unarmed (text-fig. 2). The endopodite of the 1st maxilliped is five-jointed, the second joint being the longest (text-fig. 5). The exopodites of the 1st and 2nd maxillipeds end in a group of four short-pointed setæ arranged side by side (text-fig. 5). There is a large branched pigment-spot on the ventral side of the abdomen between each pair of segments and a small circular patch of pigment on the distal end of the protopodite of the 1st maxilliped (text-figs. 1 & 2).

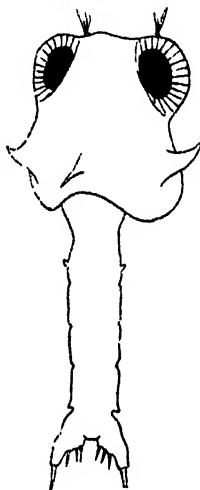
Comparison with the description given by Moreira [1912] for

Text-figure 1.



Lateral aspect of 1st zoea of *Cardisoma armatum*. $\times 88$.

Text-figure 2.



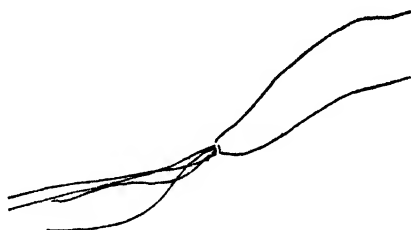
Dorsal aspect of 1st zoea of *Cardisoma armatum*. $\times 88$.

the zoea of *C. guanhumi* shows only one marked difference. In *C. guanhumi* it is stated that the cephalothorax is provided solely with a dorsal spine, the anterior and lateral spines being absent. Between two such nearly related forms as *C. guanhumi* and *C. armatum* it would not be expected that such a difference would occur. However, the figures illustrating Moreira's paper suggest that a re-examination of the South-American form might be desirable.

An account of the 1st zoea of *Gelasimus* by Hyman [1920] indicates a close similarity with the zoea of *C. armatum*. In this form, however, there are no lateral spines on the cephalothorax, although the anterior spine is present.

Among twenty or thirty larvæ preserved for examination it was noticed that two specimens differed from the rest in the form of the 1st and 2nd maxillipeds. In these two specimens the exopodites, instead of ending in four short spines as in all other specimens, ended in a brush of four plumed hairs, each about the length of the remainder of the endopodite. In both *C. guanhumi*

Text-figure 3.



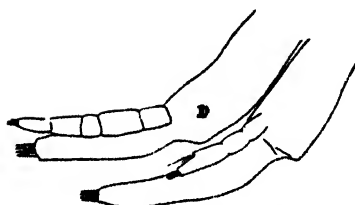
1st antenna.

Text-figure 4.

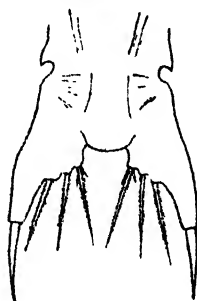


2nd antenna.

Text-figure 5.

1st and 2nd maxillipeds,
seen from inside.

Text-figure 6.



Telson.

and in *Gelasinus* the exopodites of the maxillipeds normally end in a similar structure. It cannot be said with any degree of certainty what this represents. It may be that in these two specimens the 1st zoea has already developed characters that would normally appear on a later instar, but, as no specimen was

reared to the second larval stage, this cannot be verified. It is interesting to note in this connection that Miss Webb [1919], in the larvæ of *Upogebia*, found two distinct forms. The difference in this case concerned the number of exopodites furnished with swimming setæ occurring on the thoracic legs, and became first evident at the commencement of the 2nd larval stage. Possibly the case recorded here is an analogous case of polymorphism.

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3. On the Linguatulid Arachnid *Raillietiella furcocerca*
[Diesing, 1835] Sambon, 1922. By GEORGE S.
GIGLIOLI, M.D. Pisa.

[Received November 1, 1922: Read February 6, 1923.]

This species was described by Diesing in 1835 under the name of *Pentastoma furcocercum*, from specimens collected by Natterer in South America. His original description, translated from the German, runs as follows:—

"The worms are from 9 to 10 lines in length; 1 line thick at the anterior extremity, $\frac{1}{2}$ at the posterior. They are grey in colour, while their internal organs, which can be seen in transparency, are brown and somewhat marked in white and reddish. The body is spindle-shaped and presents a linear annulation, which is most marked at the middle part of the body, while it gradually disappears towards the two extremities. On each ring are numerous stigmata disposed along a line at regular intervals. The cephalic extremity is somewhat flattened and is obtusely triangular. At its apex it presents the oval oral opening. The hook-pouches, which are situated symmetrically behind the mouth, are borne by obtusely conical structures. Each pouch is protected by three rounded pads, two lateral and one median, which is situated over the hook. Each pouch contains two hooks, probably united at their base; they are situated one over the other. The upper one is nearly straight and short; the lower one is longer and more medially directed. The posterior extremity is bifid. The male can be distinguished from the female by the penis, situated on a papilla on the mid-ventral line on the first anterior ring. I have found the two caudal points divergent in a female, but the two sexes are similar in size."

Later, in his 'Systema Helminthum,' Diesing again describes the same species under the name *Pentastoma bifurcatum*:—

"*Corpus* subfusiforme retrorsum attenuatum, extremitate caudali bifurcatum, annulato-plicatum. annulis linearibus. *Caput* obtuse triangulare depressiusculum. *Os* ovale margine lato calloso apice truncato, inter bothria obtuse triloba in formam coni truncati disposita situm. *Hamulis* inæqualibus. Long. fem. 9-13''; crass. antice ultra 1''; postice $\frac{1}{2}$ ''". Femina cauda sua bifurcata, in aliis emarginata, marem multo minorem et graciliorem sub coitu probabiliter excipit."

In 1898 Sir Arthur Shipley, in his monograph on Linguatulidæ, reproduced Diesing's description under the name *Porocephalus bifurcatum*.

In 1910 Sambon included this species in the genus *Raillietiella*, and, following the rule in zoological nomenclature, again adopted

the original specific denomination given by Diesing in 1835, so that this tongue-worm is now known under the name of *Raillietiella furcocerca*.

Through the kindness of Dr. Khalil, of the Department of Helminthology of the London School of Tropical Medicine, I have been able to examine two female specimens of this parasite, collected from the lungs of an *Amphishæna alba*, which died in the London Zoological Gardens, and I would now submit the following as a more accurate description of the external morphology of this species:—

Length 26 mm.; breadth 1 mm. (anteriorly). The cephalothorax is the bulkiest part of the body, and from it the abdomen tapers gradually towards the caudal extremity. The body is straight and delicate. The cephalothorax is roughly triangular in shape, with the generic characters of *Raillietiella* very well marked. The mouth is terminal, but situated on the ventral surface. The oral papilla is shield-shaped and large, with a well-marked chitinous outline. It is surmounted by two small rounded papillæ, which are terminal. Laterally, and slightly dorsally to these, other two long finger-shaped papillæ are situated, which are directed laterally. These structures occupy the apex of a large fleshy cone which forms the anterior part of the cephalothorax, and is very slightly flexed ventrally. At its base the anterior pair of hooks are situated. The whole chitinous hook-apparatus is remarkably small, especially the root. They are supported, or rather enclosed, by a voluminous fleshy structure, which protrudes laterally, so that when the hook is at rest not even its tip is free. The hooks are, in fact, only visible by transparency. Their fleshy base presents a somewhat complicated form, in which three parts can be distinguished: an external rounded pad or mass situated laterally to the hook and slightly behind it; a similar but smaller structure symmetrically situated on the internal aspect of the hook; and a compressed, transparent hood, situated over the two preceding organs, and which shrouds the hook, both root and blade. The hood is open at its lower end, so as to allow the extrusion of the hook-blades, but these are so small that only a very little part of the blade can ever be freed from its fleshy sheath. The hooks are smooth and simple, the posterior pair slightly larger, and supported by a much larger and stronger base. As in other species of the genus *Raillietiella*, the large sensory papillæ, corresponding to the anterior or medial pair of hooks, are finger-shaped and of unusual size, and situated on the latero-dorsal surface of the cephalothorax. Behind these and a little nearer to the median dorsal line two other smaller papillæ are visible. These I have not observed in other species (*R. boulengeri*, *R. geckonis*).

The abdomen is fairly cylindroid in its anterior third, and then tapers gradually to the posterior extremity, which is acuminate and bifid. The annulation, though present, is practically effaced, so that the number of rings cannot be given. On the first five

body-rings very distinct acuminate papillæ are symmetrically situated on the latero-ventral margin. The genital opening is on the mid-ventral line on the first body-ring. The cuticle covering the body is studded with small eminences which give it a rough appearance, particularly evident on the large papillæ. The body-wall being very fine and transparent, some anatomical characters can be made out:—

The intestine is straight and dorsal; it receives the short arcuate œsophagus slightly behind its anterior end, and opens dorsally by the anal orifice, which is situated between the two caudal appendages. The spermathecæ are rounded and symmetrically situated a little dorsally to the vagina, which opens through the anterior genital pore. The uterus is an ample sac which fills the whole body-cavity from the spermathecæ to the caudal extremity and partly embraces the intestine. It is full of eggs. On the internal surface of the body-wall the parietal gland-cells can be seen arranged in small clusters or nests; they are situated in a more or less regular annular series, two or more to each ring. The specimens described by Diesing evidently were not mature, as appears from the double hooks. Moreover, many of them were found not in the lungs, but in other organs of their hosts; they were therefore probably still migrating through the tissues to the lungs.

The hosts in which Natterer found the specimens described by Diesing are not many, but they belong to different orders; Diesing, in fact, gives three snakes: *Coluber lichtensteini*, *C. flaviventris*, *Boa constrictor*, and a lizard, *Amphisbæna flavescens*. As I have already observed in other papers dealing with this group of parasites, the genus *Raillettiella*, differing from all the others of the family Linguatulidæ, comprehends species of parasites coming from hosts of very different families: from Ophidia, Lacertidæ, and Amphibia.

According to Diesing *R. furcocerca* is to be found both in several snakes and in a lizard of very peculiar habits, the *Amphisbæna*. Although until now there is no direct evidence to the contrary, I think it improbable that the same species should inhabit such different hosts. For this reason I have thought it well to give a more complete description of this parasite, so that comparison may be made with specimens obtained from snakes.

Although several species of *Raillettiella* have been described, both in the adult and semi-adult forms, we have as yet no knowledge of the younger developmental forms, nor of the intermediary hosts in which they live. Hitherto the majority of intermediary hosts for those members of the family, at least, which are found in snakes, have been mammals; a large variety of mammalia have often been found to act as intermediary hosts to the same species of parasite. *Armillifer amillatus*, according to Noc, has been found at its larval stage in 36 species of mammals. Other species, parasitic in crocodiles, have in all probability fish as their intermediary host. It is probable that all these immature forms,

given under a variety of names, such as *P. gracile*, *P. crocodili*, and others, generally found in fish of the families Gymnotidæ, Characinidæ, and Siluridæ represent larval stages of the Sebekini. Moreover, the feeding-habits of their definite hosts render this hypothesis extremely probable. The same is probably the case with the genus *Reighardia*.

Many animals, in which tongue-worms of the genus *Raillietiella* have been found, are purely insectivorous in their feeding-habits. For example, the lizards of the genus *Calotes* and *Gecko* (*R. geckonis*), *Amphisbæna alba* (*R. furcocerca* (Diesing)); and the Amphibian, *Bufo melanostictus* (*R. indica* (Gedoelst, 1921)).

If even in the genus *Raillietiella*, as in all the others, there exists a biological cycle which evolves in two different hosts, it will be interesting to see in what intermediary host the larval forms of these parasites of insectivorous animals pass their existence, and how they manage to get into their definite host. Could the intermediary host of *Raillietiella* be an invertebrate animal?

4. The Permian Fishes of the Genus *Acentrophorus* *. By
E. LEONARD GILL, M.Sc., The Royal Scottish Museum,
Edinburgh.

[Received June 6, 1922 : Read February 6, 1923.]

(Text-figures 1-16.)

Introductory.

As the earliest known members of the family Semionotidæ and the only Palæozoic Actinopterygians of a higher grade than the Chondrostei, the small fishes named *Acentrophorus* by Traquair (1877), found in the Permian of the County of Durham, have frequently been referred to and discussed in palæontological writings. An examination of the abundant material in the museums at Newcastle and Sunderland showed that it would be possible to add considerably to what was hitherto known of the structure of these fishes, and the main results of such an examination are here given.

The first species of *Acentrophorus* to be named and described was *A. glaphyrus*, which Agassiz published (1835) as a species of *Palæoniscus*. It is found in the Marl Slate, the lowermost bed of the Permian series in Durham and Northumberland, but as it is rare and not well preserved it has furnished little information as to the structure characteristic of the genus. A much more abundant and better preserved fish is *A. varians* from the Upper Magnesian Limestone. It was described as *Palæoniscus varians* by J. W. Kirkby (1862 and 1864), who at the same time described two much scarcer species occurring in the same beds, "*Palæoniscus*" *altus* and "*P.*" *abbsi*. Reasons are here given for doubting whether the species *abbsi* ever had a real existence. In 1873 Lütken pointed out that these fishes were wrongly assigned to *Palæoniscus*; and in 1877 Traquair established for them the genus *Acentrophorus*.

Kirkby's account (1864) includes a careful description of the general proportions, the squamation, and the fins. Traquair added many details, especially in regard to the osteology of the head. In a few minor points, however, the material at his disposal evidently led him astray, and it does not appear to have shown him anything of the teeth, the axial skeleton, or the bones supporting the fins. Few figures of the fishes now included under *Acentrophorus* have been published, and none give a very clear representation of their structure. The specimens, from both the Magnesian Limestone and the Marl Slate, seem to have

* Communicated by D. M. S. WATSON, M.Sc., F.R.S., F.Z.S.

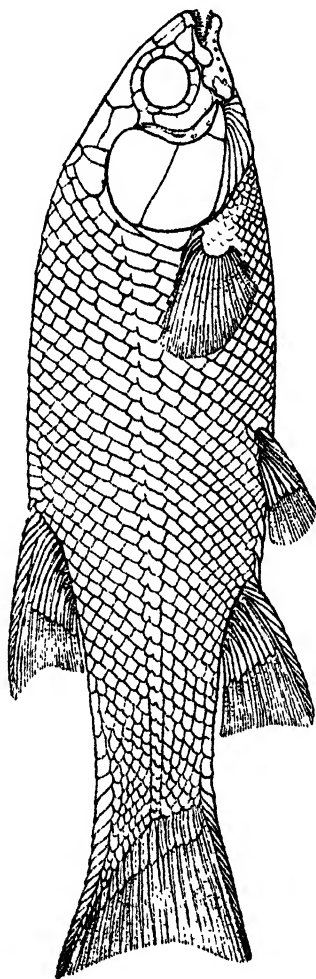
been fossilised under quiet conditions; the parts are rarely much disturbed and practically never scattered. On the whole this is a disadvantage. The scales and the few strong bones (frontal and angular for example) are often well preserved, but most of the bones are delicate, and as they are crushed one upon another it is usually very difficult to make out their boundaries. In the case of the palate it is practically impossible. The distal parts of the fin-rays, too, are hardly ever shown satisfactorily. It is only through having abundant material for comparison that it has been possible to make out even so much of the skeleton as is here described.

Description of the Genus.

The descriptions already given by Kirkby, Traquair (1877, pp. 563-4), and Dr. A. Smith Woodward (1895, p. 51), together with the restorations and other figures accompanying this paper, render it unnecessary to go into much detail as to the main external features characterising *Acentrophorus*. The general shape (text-fig. 1), including the excavation of the back along the base of the dorsal fin, is much as in *Lepidotus*, except that the snout is blunter. To judge by the number and appearance of the specimens that have been compressed dorso-ventrally, the body was fairly rounded. The scales, compared with those of most Semionotids, are thin; they overlap deeply, nearly half of each scale being covered by the one in front of it. Their only ornament is a series of concentric lines near the hinder margin; these are presumably annual growth lines, and as many as five can sometimes be counted. The absence of a row of dorsal ridge-scales with projecting points is the character upon which Traquair separated the genus from *Semionotus*; in place of points these scales often even show a concave hind border. But the most striking characteristic of the squamation is the great though perfectly graduated variation in the size of the scales on different regions of the body, and particularly the great depth of the anterior scales of the lateral line. In shape the lateral line scales are not unlike those of *Dapedius*. The lateral line can usually hardly be followed on the outer surface in *A. varians* and *altus*, except by the notching of the scales. In *A. glaphyrus* it is more prominent; and on the inner face of the scales it is marked by a conspicuous groove in all the species. Peg-and-socket articulation is well developed on the inner face of the anterior scales of the upper part of the flanks (text-fig. 2, A); but it is absent in *A. varians* from the smaller scales of the lower flank, and dies out gradually even in the upper scales as they are traced backward towards the tail-shaft (text-fig. 2, B, C, D). In *A. altus* and *A. glaphyrus* the scales have on the inside a low rounded ridge, which is continued above into the peg (text-fig. 2, E), and in these species the peg-and-socket articulation extends almost or quite to the tail. In all the species the scales on the jugular region are very small and rounded (text-fig. 7, *sc.*). As in many other Semionotids, there

are three or four enlarged scales in the mid-ventral line immediately in front of the anal fin. Enlarged ridge-scales mark the mid-dorsal and mid-ventral line of the tail-shaft. As they near the caudal fin they become pointed posteriorly, and pass without a break into the upper and lower series of tail fulcra.

Text-figure 1.



Acentrophorus varians. Restoration.

About one-and-a-half times natural size.

The massive development of the fin fulcra is a striking characteristic of the genus. In the two later species, *A. varians* and *A. altus*, each fulcrum fits closely to the point over the one next behind it; in the Marl Slate species, *A. glaphyrus*, the points are considerably more drawn out and tend to project more freely.

The smaller fulcra are paired, but the larger ones at the base of each series are single, the transition taking place through the deepening of a median groove. The pectoral fin has only three (possibly sometimes four) fulcra, the distal half of its upper border being unprotected (text-fig. 9).

Of the fins themselves, two features are particularly noteworthy: the situation of the pectoral fin and the degree of heterocercy of the caudal. The pectoral fin is placed rather high on the flank, and (at least in *A. varians* and *A. altus*) its lobe is so formed that the fin can only be spread over or abreast of the lower flank scales. It could not in life be spread below the level of the body as in other fusiform Semionotids, with the pre-axial border turned forwards and downwards. It is occasionally fossilised in this position, but it is then seen to be unnaturally forced down so as to point forward over the jugular region or the branchiostegal rays.

The dorsal body-lobe of the tail is in a particularly interesting stage of reduction. It still extends to the extreme upper tip of the tail, but for about the latter half of the distance it is represented by only a single line of small scales. Towards the tip these scales are so small that but for their slightly different shape they closely resemble the joints of the minute first dermal ray lying beside them. (The appearance suggests the possibility that on the withdrawal of the notochord these little scales might be directly converted into the joints of an additional dermal ray.)

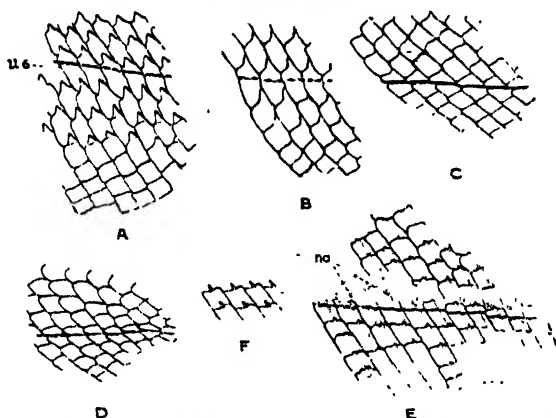
In other respects the fins greatly resemble those of *Lepidotus*. As in that genus, a considerable length of the proximal part of the rays is unjointed. In the best-preserved examples these unjointed lengths and some of the joints immediately following them show a flange-like lateral expansion, which led Kirkby to state that they were covered by an accessory scale. The flanges are especially conspicuous in the anal fin, where the rays are few (only five or six behind the fulcra) and widely spaced.

It is impossible to make out completely the bony structure of the head, since none of the specimens show the elements scattered, and all the more delicate parts are crushed together into a fragile, semi-transparent plate no thicker than fine notepaper. Thus of the chondrocranium it can only be said that in the hinder part it was considerably ossified, and that in one or two examples a pair of exoccipitals are seen, and in another a club-shaped bone in the position of the epiotic. A small bony rod occasionally seen in front of the upper end of the pre-operculum may very probably be the alisphenoid (text-fig. 7, *asp.*).

Other internal bones of the skull are often shown, but never in such a way that they can be completely described. The front of the parasphenoid is very commonly seen as a straight rod crossing the orbit (text-figs. 6 and 13); it has a lateral flange beginning a short distance behind its anterior end, but its hinder portion remains unknown. The vomers are separate, in front

at least, but their connexion with the parasphenoid is not clearly seen. Below the parasphenoid are the crushed remains of the palatal bones, of which it can only be said that a thickened lower border represents the palato-pterygoid bar, and that the shape of the metapterygoid and quadrate can sometimes be roughly made out. The metapterygoid has a central, upwardly directed process (as in *Lepidotus*, *Amia*, etc.) for articulation with the otic region of the brain-case. Traquair stated that "a well-marked quadrate is distinct enough," but if he was not mistaken he must have seen some exceptional specimens. A symplectic with a rod-like stiffening lies just inside the lower end of the preoperculum,

Text-figure 2.



Outlines of scales of *Acentrophorus* seen from the inside; about twice natural size.

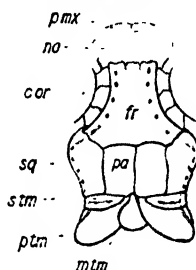
All the figures except F include scales of the lateral line. A-D. *Acentrophorus varians*: A, anterior scales (l.s. sixth lateral line-scale); B, half-way between occiput and dorsal fin; C, between dorsal and anal fins; D, last scales of lateral line, with others above and below. E. *A. altus*, scales above anal fin (na., remains of neural arches and spines). F. *A. glaphyrus*, scales below lateral line between pelvic and anal fins.

its anterior end overlying the quadrate. Projecting from under the upper end of the preoperculum some part of the hyomandibular is often seen; it is well ossified, and in shape closely resembles the hyomandibular of *Lepidotus*. All these bones, in so far as they can be made out, are shown in text-fig. 11. Of the hyoid apparatus, the anterior part of the ceratohyal and the small hypohyal are frequently shown. The ceratohyal is deep, especially at its fore end; the hypohyal is knobbed and rather strongly ossified. In one small specimen of *A. varians* from the Kirkby collection the operculars are somewhat displaced, and in the gap thus left three delicate branchial arches are seen.

The membrane bones forming the exterior of the skull are

much more satisfactorily preserved. Those of the cranial roof are shown in outline in text-fig. 3. The pair of parietals together roughly form a square. One well-preserved example of *A. altus* shows two parietal ossifications on each side (text-fig. 4), but as other specimens have only one, this is presumably no more than an occasional aberration. The parietals are flanked by "squamosals" (pterotics, supratemporo-intertemporals) which have a rounded expansion of the outer border anteriorly. The frontals are fused into a single plate, the strongest bone in the whole skeleton with the exception of the cleithrum; it is nearly always found either turned outwards clear of the head or folded down beneath it, rarely crushed together from side to side. It is wide behind and much narrowed in front, the very large orbits producing deep excavations of its lateral margins. Three of the circumorbitals adjoin each of these excavations. The nasals are so delicate that though their extent is seen, their exact shape cannot be made

Text-figure 3.



Outline restoration of skull-roof of *Acentrophorus varians*. About one-and-a-half times natural size. *c.or.*, circumorbitals; *fr.*, frontal; *m.tm.*, median temporal plate; *na.*, nasals; *pa.*, parietals; *p.mx.*, premaxillae; *p.tm.*, post-temporal; *sq.*, squamosal; *s.tm.*, supratemporal.

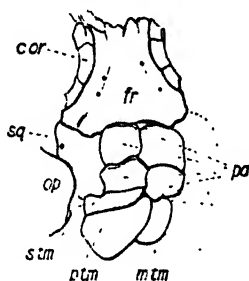
out, chiefly because they are crushed down on the comparatively strong backward processes of the premaxillae. In some specimens there is a suggestion of a small median "ethmoid" and of separate lateral ossifications (either prefrontals or adnasals). The edge of what may be a postfrontal sometimes appears under the anterior border of the squamosal. A pair of very large scale-like post-temporals adjoin the hinder margin of the parietals and squamosals, the suture being overlaid by a transverse pair of supratemporals (extrascapulars). A smaller median plate (text-figs. 3 and 4, *m.tm.*) is wedged in between the post-temporals; it usually overlaps one of them, and is overlapped by the other. It perhaps belongs to the supratemporal series.

The large orbit is surrounded by a chain of about ten circumorbitals, of which those forming its posterior boundary are much narrower than the rest. Between the circumorbitals and the preoperculum there were probably thin cheek-plates, but their

presence is suggested only by faint radiating grooves crossing the bones of the palate in a few specimens. One or two examples show a triangular bone which apparently covered the space in front of the orbit between the nasal and the maxilla.

The opening of the mouth is very small. It is bounded above by fairly strong paired premaxillæ, each supported by a strong process running backwards beneath the nasals to the frontal (text-fig. 5, *r.pmar.*). The maxillæ are short and delicate; their slender anterior portion passes inward behind the premaxillæ; posteriorly they are expanded to overlie the lower jaw about the middle of its length. The lower jaw is remarkable chiefly for the fact that in this early genus it has already acquired in the fullest degree the peculiar shape characteristic of the Mesozoic Semionotids and Macrosemiids. As in these later fishes it is very deep behind and shallow in front, with a downward curve in the region of the symphysis. The agreement extends also to

Text-figure 4.



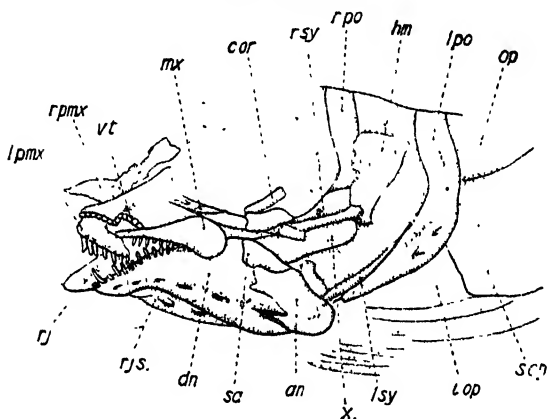
Acentrophorus altus. Skull-roof of a specimen with four parietal plates. In the Kirkby Collection, Hancock Museum. The plates behind the frontal are slightly displaced to the right. About one-and-a-half times natural size. Lettering as in text-fig. 3, with *op.*, operculum.

the shape of the constituent bones, at any rate to those encasing the outer side of the jaw—the angular, coronoid and dentary (text-figs. 1, 5 and 6). An articular ossification was probably present, but though it is sometimes suggested it is not clearly shown. Many specimens show something of the inner side of the jaw, but the splenial was apparently very thin, and its boundaries are lost. The most conspicuous feature exhibited on the inner face of the jaw, as it is actually preserved, is a row of protuberances near the lower margin corresponding to the sensory pits in the outer face of the dentary (text-figs. 5 and 13).

The only mention of teeth in *Acentrophorus* occurs in Dr. Smith Woodward's Catalogue (1895, pp. 51 and 52). Traquair states that he found none, and Kirkby's account makes no mention of any. It is evident, however, that Kirkby had discovered them subsequently, for the fine specimen represented in text-fig. 5 bears

a label in his writing with the word "teeth." As a matter of fact, a considerable proportion of all the specimens exhibit teeth or some trace of teeth when they are examined with sufficient magnification and suitable lighting. Text-figs. 5 and 6 taken together show the dentition fairly completely. Long styliiform teeth are borne by the premaxilla, the narrow shaft of the maxilla, and the anterior half of the dentary. The foremost teeth on the dentary are especially long and curved, and it is these that are most frequently found preserved. A single specimen suggests, though not conclusively, that there were minute teeth on the splenial. The vomer is bordered by short, very

Text-figure 5.



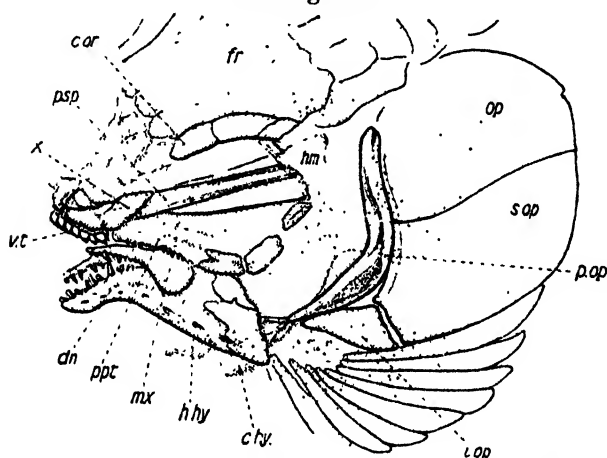
Acentrophorus varians. Head showing dentition; Kirkby Collection, Hancock Museum. About four times natural size. *an.*, angular; *c.or.*, circumorbital; *dn.*, dentary; *hm.*, hyomandibular (part); *i.op.*, interoperculum (space left by it); *l.po.*, left preoperculum; *l.pmx.*, left premaxilla; *l.sy.*, left symplectic; *mx.*, maxilla; *op.*, operculum; *r.j.*, right ramus of lower jaw; *r.j.s.*, probably right splenial, displaced; *r.pmx.*, right premaxilla; *r.po.*, right preoperculum; *r.sy.*, right symplectic; *sa.*, coronoid (supra-angular); *s.op.*, suboperculum; *vt.*, vomerine teeth; *x.*, possibly the right ceratohyal.

stout teeth; they usually have the appearance of rounded knobs, but the best examples show them to have had short conical points. In one specimen that seems to show the buccal surface of the vomers, there is a suggestion of inner rows of stud-like tritoral teeth, but they are too obscure to warrant a positive statement. A few specimens, notably the one from the Sunderland Museum represented in text-fig. 6, show that the palatopterygoid also bore small conical teeth.

The opercular apparatus is remarkable in the same way as the jaws, namely in that it is so typically of the Semionotid pattern. Text-fig. 6 and the restorations make its composition clear

without further description. One or two remarks only are necessary. The suture between the opercular and subopercular plates varies considerably in position, but nearly always leaves the suboperculum as the larger bone, except in *A. glaphyrus*. The branchiostegal rays number nine or ten on each side (text-fig. 7). (Traquair thought there were "few, about seven.") Traquair suspected the presence of a gular; if there was a gular, however, it must have been a very delicate plate, for in the numerous specimens that ought to show it there is no definite trace of it. The only example which does show anything that could well be taken for a gular is Kirkby's type-specimen of

Text-figure 6.



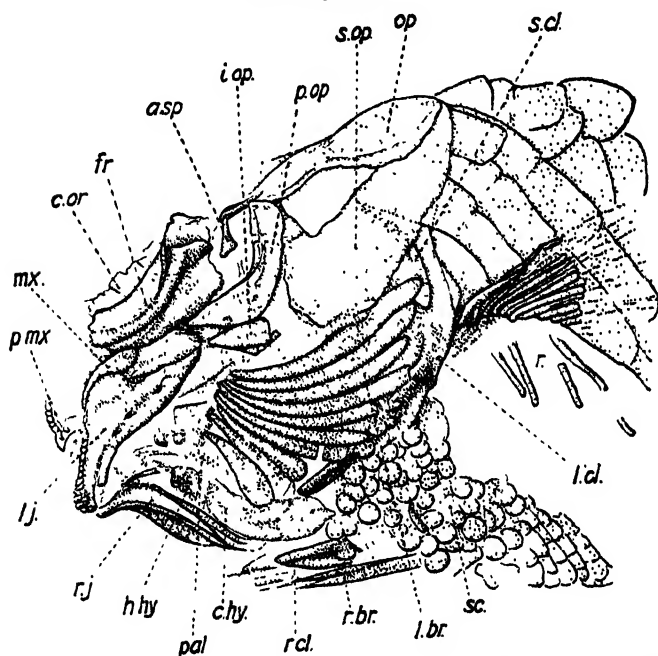
Acentrophorus altus. Head showing dentition; Sunderland Museum. *c.hy.*, ceratohyal; *c.or.*, circumorbitals (three bordering frontal, three more between parasphenoid and lower jaw); *dn.*, dentary; *fr.*, frontal; *h.hy.*, hypohyal; *hm.*, hyomandibular; *i.op.*, interoperculum; *mx.*, maxilla; *op.*, operculum; *p.op.*, preoperculum; *p.pt.*, palato-ptyergoid with teeth; *p.sp.*, parasphenoid; *s.op.*, suboperculum; *v.t.*, vomerine teeth; *x.*, left premaxilla, or possibly the body of the vomer. About four times natural size.

A. altus, the head of which is represented in text-fig. 13. The plate marked *x* in this figure is a thin, detached bone, of much the size and shape that the gular would have to possess.

The opercular bones and the roofing bones of the head are ornamented with fine vermicular raised lines. The course of the principal sensory canals of the head can be traced fairly completely. The nasal bones are too thin and badly preserved to show pits or grooves, but the frontal often shows a line of four pits on each side near the orbital margin, and grooves and pits carry the line backwards along the outer side of the squamosal to cross the outer end of the supratermporal and the antero-

external angle of the post-temporal. From thence it crosses the supraclavicle obliquely to the first scale of the lateral line series. The under surface of the frontal is marked by a conspicuous ridge on either side parallel to the curved orbital margin. It underlies the line of sensory pits and may be connected with their canal, or it may only be a boundary wall for the chondrocranium

Text-figure 7.



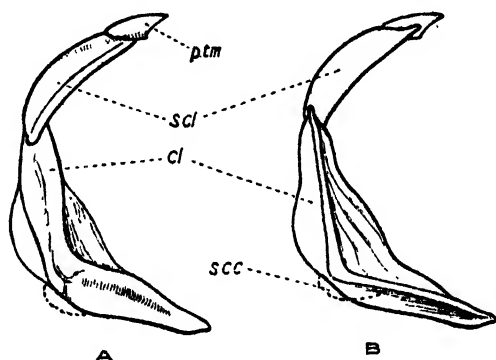
Acentrophorus varians. Head crushed obliquely from the left side and from below, showing branchiostegal rays and parts of shoulder-girdle; Kirkby Collection, Hancock Museum. About four times natural size. *asp*, alisphenoid; *c.hy.*, right ceratohyal; *c.or.*, circumorbitals; *fr.*, frontal, left side from below; *h.hy.*, right hypohyal; *i.op.*, interoperculum; *l.br.*, left branchiostegals; *l.cl.*, part of left cleithrum; *l.j.*, left lower jaw; *mx.*, maxilla; *op.*, operculum; *pal.*, bones of palate; *p.mx.*, premaxilla; *p.op.*, preoperculum; *r.*, ribs; *r.br.*, right branchiostegals; *r.cl.*, point of right cleithrum; *r.j.*, right lower jaw; *s.o.*, small scales of jugular region; *s.cl.*, supraclavicle, displaced; *s.op.*, suboperculum.

in this region. As in *Amia*, one of the pits on the squamosal forms a notch in the margin of the bone at the point where the main canal was joined by the branch traversing the preoperculum. The supratemporals are strongly grooved and pitted by the transverse branch of the canal. The situation of all these pits

and grooves is indicated in text-fig. 3. On the side of the head the sensory canals can be followed even more clearly. Three or four pits are usually conspicuous in the length of the preoperculum, and from the lower end of this bone the line is continued by a groove across the angular, and by a chain of six or seven well-marked pits along the dentary near its lower border (text-figs. 5 and 6). Finally, there are longitudinal grooves on the inferior circumorbitals, probably marking the course of a suborbital canal.

The pectoral girdle is rarely seen at all completely, being largely covered as a rule by the operculars and branchiostegal rays. Its general shape, however, can often be seen through these bones (text-figs. 7 and 14), and more or less of the thickened portion of the cleithrum ("clavicle"), ornamented by fine transverse raised lines, appears normally along the lower edge of the

Text-figure 8.



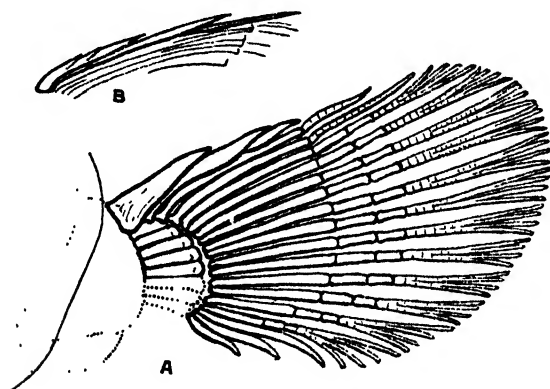
Outline restoration of shoulder-girdle of *Acentrophorus varians*. A., right side, external view; B., left side, internal view. Double dotted line shows course of lateral line. *cl.*, cleithrum; *ptm.*, post-temporal; *s.c.c.*, position of scapulo-coracoid cartilage; *s.cl.*, supraclavicle. About three times natural size.

suboperculum. Occasional specimens show some portion of the girdle more fully, especially from the inner side, and make possible such a restoration as is given in text-fig. 8: The large scale-like post-temporal has already been referred to. The supraclavicle, which normally appears in part behind the operculum, is of simple, slightly curved form, strengthened along its anterior edge. The cleithrum is massively thickened externally in a boomerang form, pointed at either end, and with a band of fine transverse raised lines marking the portion which sometimes appears at the surface below the suboperculum. Its inner face is expanded and flattened, especially about the middle of its length, but this face also bears a rod-like thickening, bent almost

at a right angle just above the area of attachment of the scapulo-coracoid cartilage. This latter cartilage has left a distinct trace of its form in two or three of the specimens (text-fig. 9). Many specimens show the pointed lower ends of the two cleithra meeting (or slightly displaced from their normal contact) in the midventral line, and prove the entire absence of an infra-clavicle.

The skeleton of the pectoral fin of *A. varians* is shown in text-fig. 9. The radials are about eight in number. They appear as a single series, though slight cups shown in their outer ends may have lodged minute distal cartilages. The first fin fulcrum, which is large, seems always to be based directly on the scapular cartilage in series with the radials. There is no sign of the

Text-figure 9.



A. Skeleton of left pectoral fin of *Acentrophorus varians*. Dotted lines show the approximate shape of the scapulo-coracoid cartilage and of three postaxial radials which have only been seen as impressions. From a specimen in the Kirkby Collection and one in the Sunderland Museum.

B. Part of preaxial edge of pectoral fin of *Acentrophorus glaphyrus*, showing the long, slender fulcrum. From a specimen in the Kirkby Collection, Hancock Museum. Both figures about four times natural size.

presence of a metapterygium. The dermal rays are about twice as numerous as the radials, and where it happens that two adjacent rays are supported by one radial, the bases of these rays are noticeably inclined together. The two first (pre-axial) rays are unbranched, and the three last (post-axial) are both unbranched and unjointed. The remaining rays are all forked twice in the distal third of their length.

The pelvic fins are very short-based, and are remarkable externally for the great length attained by one of the fulcrum (text-fig. 10, B). Specimens in which the inner surface of the scales is exposed not infrequently show the supporting bone of the

pelvic fin. The best example of this kind, showing both supports together, is represented in text-fig. 10; the bones are seen to be of the same general pattern as in *Lepidotus*, but of a stouter form. Nothing is seen of any radials intervening between the supports and the dermal rays, though the parts are so small and difficult to see that no definite statement on the point can safely be made.

Previous investigators do not appear to have noticed any traces of the axial skeleton of the trunk, except that Kirkby refers to the supports of the median fins. The distal ends of these supports fairly often appear, where scales are missing along the bases of the fins. But much more than this can be made out in certain specimens, particularly where, as occasionally happens,

Text-figure 10.

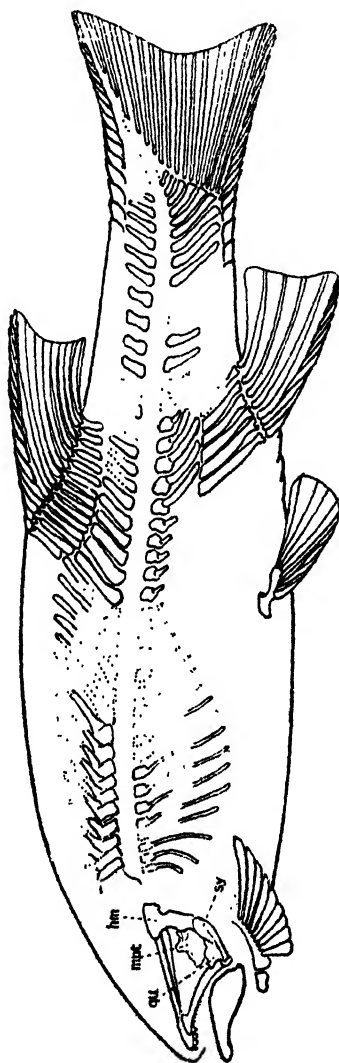


- A. Pair of pelvic fin-supports of *Acentrophorus varians*, lying on the inner face of disturbed scales.
 B. Part of pelvic fin of *Acentrophorus varians*, showing basal fulcra. Both figures from specimens in the Kirkby Collection, Hancock Museum; about four times natural size.

the splitting of the matrix has cleanly separated a right and a left half, leaving the inner surface of the scales completely exposed. (Such specimens sometimes show by a difference of colour the exact outline of the abdominal cavity, which is precisely as in a herring or similar fish.) If a specimen such as this is examined with a suitable lens and in a strong, very oblique light, any break in the regularity of the scale pattern being carefully scrutinised, it will almost always be found to show more or less extensive traces of the axial skeleton. Kirkby's collection in the Hancock Museum at Newcastle contains three specimens of this nature in which the skeleton is particularly well shown, and the information they give is set out in text-fig. 11, where the unbroken lines represent the parts which are actually seen. The

bones are represented in the fossils by little flattened, semi-transparent pieces of a substance resembling sugar-candy. They were probably not very strongly calcified, and the flattening may

Text-figure 11.



Axial skeleton and other internal bones of *Acentrophorus varians*, from specimens in the Kirkby Collection, Hancock Museum. About one-and-a-half times natural size. *hm.*, hyomandibular; *mpt.*, metapterygoid; *g.*, quadrate; *sy.*, symplectic.

have expanded their shape to some extent, but a comparison of different parts does not suggest that much allowance need be made for alteration of this kind.

The number of vertebral segments seems to agree closely with the number of rows of scales—about forty in each case from the head to the middle of the base of the caudal fin—but the longitudinal spacing does not correspond by any means. In the caudal region the segments are so widely spaced as to suggest some sort of foreshadowing of the alternate pleuro- and hypo-centra found in the same region in such fishes, for example, as *Amia*. But there is no sign of actual centra; the notochord evidently persisted complete. The interpretation of what is seen of the vertebral column is not easy. In the segments close behind the head it rather strongly suggests the vertebral column of the sturgeon. It appears as though in the anterior segments the neural spines may have been separate, but further back they were almost certainly fused with the arches. The spines below the dorsal fin-supports are markedly widened from front to back, a peculiar feature, which is confirmed, however, by all the specimens in which these parts are shown. In the anterior caudal region the spines seem to be wide and short; further back they are narrower again and are lengthened to support the dorsal ridge-scales. Their continuation into the tail-lobe is not shown in any of the specimens. Well ossified ribs appear in many specimens in the anterior abdominal region (*cf.* text-fig. 7), extending more than half-way from the level of the lateral line to the ventral border; but in the posterior abdominal region they are very short. They are succeeded by four or five fairly long hæmal spines, inclined strongly backwards across the upper ends of the anal fin-supports. In the posterior part of the tail-shaft the hæmal spines, like the corresponding neural spines, are lengthened to support the ventral ridge-scales, and the succeeding spines serve to support the caudal fin-rays in the usual way. The supports of the dorsal and anal fins are well shown. There is one to each fin-ray. At the front of the dorsal fin there is also a separate support for each of the fulcra that stand in series with the rays, but the corresponding fulcra of the anal fin, which are more crowded, have only one support for them all. The distal ends of all the supports are notched or forked; in the case of the dorsal fin the two heads so formed appear to share in the support of two adjacent rays. The internal ends are more or less expanded, and seem to come into close contact with the neural or hæmal spines, except perhaps in the case of those from the back of the fin. The great proportionate size of the anal fin-supports is a peculiar feature of the internal skeleton of *Acentrophorus*.

The Species of Acentrophorus.

There are known at present three indisputable species of *Acentrophorus*: *A. varians* and *A. altus* (Kirkby sps.) from the Upper Magnesian Limestone, and *A. glaphyrus* (Agassiz) from the Marl Slate. A fourth species, *A. abbsi* (Kirkby), appears to be

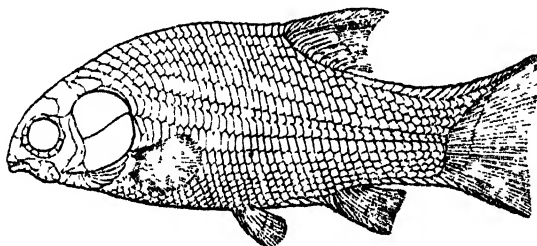
ill-founded. Text-figs. 1, 12, 13, 14, 15 illustrate the differences distinguishing these species, and will be sufficiently supplemented by the following brief notes :—

Acentrophorus varians (Kirkby). (Text-fig. 1.) The type-species and very much the most abundant. In spite of its name, not more variable than many modern fishes, *e. g.*, trout, roach. Specimens range in length from 5–11 cm.

Acentrophorus altus (Kirkby). (Text-fig. 12.) Very much scarcer than *A. varians* but occurring in the same beds. Differs only in its deeper form and, as already stated, in the character of the inner surface and articulation of the scales (text-fig. 2). Length 4–8 cm.

Acentrophorus abbsi (Kirkby). Also from the Upper Magnesian Limestone of Co. Durham. Supposed to be distinguished from the other species by its extraordinarily lengthened form. Close examination of the two or three examples in Kirkby's collection seems to show that they are no more than distorted specimens of

Text-figure 12.



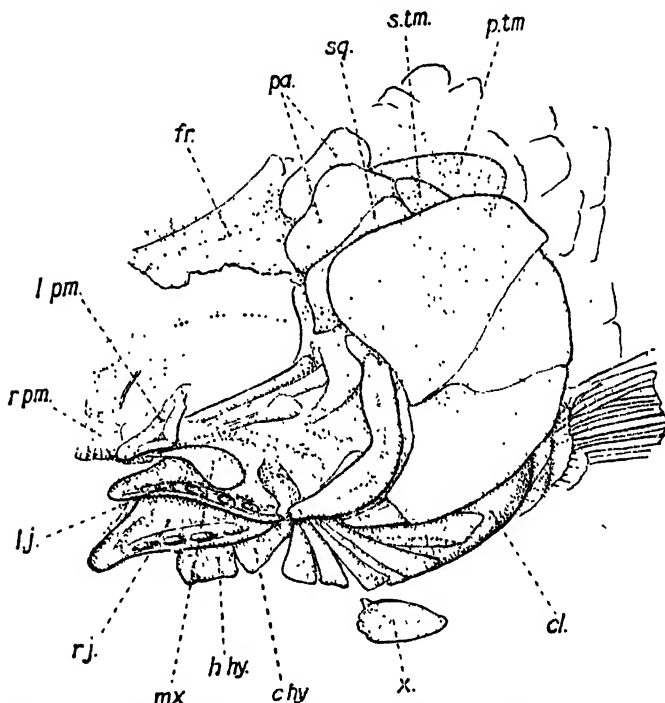
Acentrophorus altus. Restoration.
About natural size.

A. varians. Text-fig. 14 shows the head of the type-specimen. It will be seen that the parts are dragged out to a great degree longitudinally. The opercular apparatus has held together, but is lying far behind its proper position in relation to the squamosal and lower jaw, leaving the hyomandibular region widely exposed. Similarly the squamosal, supratemporal, and post-temporal are dragged apart, and the pectoral fin pulled from its connexion with the shoulder-girdle. A similar distortion is apparent in the whole length of the body, the scales hardly or not at all overlapping and in places separated altogether. Kirkby's figure (1864, pl. 18. fig. 3) shows the posterior half of the body separately; in the actual specimen the two halves are parted by a very shallow horizontal fault or slip-line which has carried them some distance asunder, with a trail of scales as their only connexion. The condition is difficult to account for, but it is evident that movement took place in the surface layer of limestone before it was quite consolidated but after the fish had

become completely macerated. In the Marl Slate occasional examples of *Palæoniscus freieslebeni* may be found in precisely the same drawn-out condition. Unless other specimens exist in which the attenuated form can be shown to be that of the living fish the species *A. abbsi* should be dropped.

Acentrophorus glaphyrus (Agassiz). (Text-fig. 15.) Found in the Marl Slate at the base of the Magnesian Limestone, and

Text-figure 13.

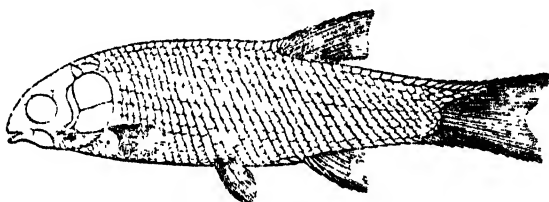


Acentrophorus altus. Head of Kirkby's type-specimen (Quart. Journ. Geol. Soc. vol. xx. 1864, pl. 18. fig. 1). About four times natural size. *chy.*, ceratohyal; *cl.*, cleithrum; *fr.*, frontal (left side broken away); *h.hy.*, hypohyal; *l.j.*, left lower jaw; *l.p.m.*, left premaxilla (part); *mx.*, maxilla; *pa.*, parietals; *p.t.m.*, post-temporal; *r.j.*, right lower jaw, inner surface; *r.p.m.*, right premaxilla; *sq.*, squamosal; *s.t.m.*, supratemporal; *x.*, possibly a gular plate.

therefore the earliest species. More variable in form than *A. varians*; some examples, the type-specimen among them, deep in the body, others shallower than the form represented in text-fig. 15. The chief diagnostic character hitherto attributed to the species is a pronounced fine denticulation of the free hinder border of the scales. This denticulation is, however, so very

as those of this fish are not well preserved in the Marl Slate; on the exposed side of a specimen they are nearly always variously splintered at the hinder border, and it is usually impossible to find a perfect scale. A single example in the Hancock Museum retains undamaged scales, and in this example, as in some in the British Museum (Smith Woodward, 1895, p. 54), the scales have the hind margin entire or at the most slightly frilled. It is therefore evident either that the denticulation is an inconstant character or that more than one species is included under the name *glaphyrus*. Against the latter possibility is the fact that the two examples showing the clearest denticulation are respectively among the deepest and the shallowest in body-form. In any case the denticulated scales do not form a reliable or useful specific distinction. Nevertheless, *A. glaphyrus* is distinguishable from *A. varians* by several well-marked characters. The caudal fin in *A. glaphyrus* is considerably longer and more deeply forked (much like that of *Palæoniscus* in fact, whereas in the later species the tail is shaped as in *Lepidotus*); the fulcra on all the

Text-figure 15.



Acentrophorus glaphyrus. Restoration.
About natural size.

fins are much longer and slenderer, with freely-projecting needle-like points; the pectoral fin is set a little lower on the body and its basal lobe is so shaped as to permit of its being turned downwards with the preaxial border in front; in the skull the frontal is wider anteriorly than in *A. varians*, and the maxilla is shorter and stouter; the lateral line is prominent externally; the inner face of the scales is ridged and the articulating pegs are narrow and finely pointed—the inner face of the scales, in fact, resembling that of *A. altus*, and still more closely that of *Palæoniscus*.

A note seems called for regarding the puzzling second figure of *A. glaphyrus* in King's monograph (1850, pl. 22. fig. 4). The original specimen is in the Hancock Museum. Behind the pectoral region it is particularly well preserved, but the head (which appears very large and "Palæoniscid" in the figure) is in reality broken up, part of the area being occupied by a good impression of the skull-roof.

A fish found in the Trias of Chicopee Falls, Mass., was described by Newberry (1888, p. 69, pl. 19. figs. 3, 4) under the

name of *Acentrophorus chicopensis*. The caudal lobe, which his figures show to be as short as in *Semionotus*, is enough, however, to prove that the fish is not an *Acentrophorus*. In addition, the scales are too uniform in size, and the general outline does not suggest *Acentrophorus* either in head or body. It should also be said that Newberry's discussion of the genus and of its relationship to "*Ischypterus*" (pp. 67-69) is on the whole misleading, since it is founded only on the obscure figures accompanying Kirkby's paper of 1864.

Another fish assigned to the genus is *Acentrophorus dispersus* Fritsch (1894, p. 81, pls. 113, 114) from the Lower Permian (Schwartenkohle) of Kounova, Bohemia. Its remains are very imperfect, but Fritsch's figures show enough of the upper and lower jaws, the opercular apparatus and the pectoral girdle to prove that in all these essential elements of its structure the fish was fundamentally different from any Semionotid. Indeed, at the end of his description of it, Fritsch himself appears to have concluded that it was a Palæoniscid.

Summary.

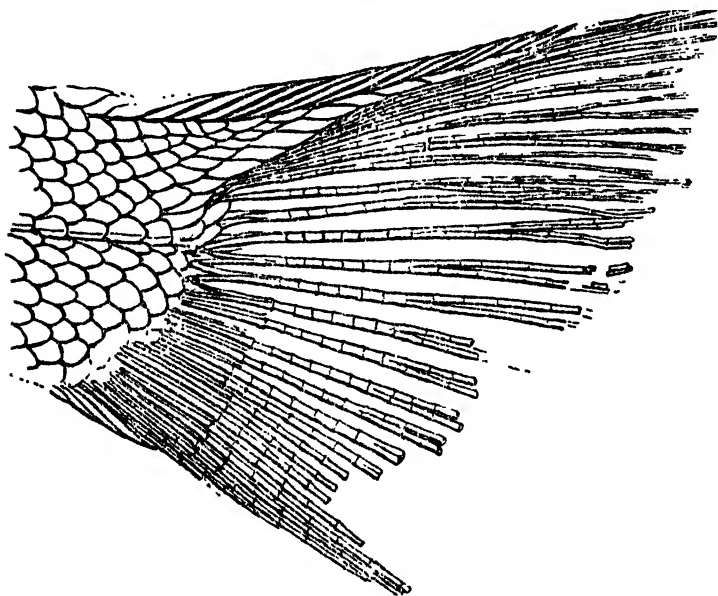
The propriety of placing *Acentrophorus* in the family Semionotidæ was not in doubt, but it is amply confirmed by the additional information now brought forward. In the exact correspondence of the dorsal and anal fin-rays with their endoskeletal supports, in the reduced maxilla, the narrow preoperculum and the whole plan of the opercular apparatus, in the absence of an infra-clavicle as in all the details of the pectoral arch and the pelvic bones, *Acentrophorus* is a characteristic representative of the Protospondyli and of the family Semionotidæ.

At the same time, *Acentrophorus* does in certain respects retain primitive characters. It seems, in fact, to provide us with something that is comparatively rarely found among fossil fishes, namely a really early representative of a new group which still shows definite traces of its origin from older types. The most striking character of this kind in *Acentrophorus* is undoubtedly the upper caudal lobe. As compared with the caudal lobe of the contemporary Palæoniscids it is certainly greatly reduced, but the reduction is only in depth; the caudal lobe of *Acentrophorus* is still of the maximum length. It is interesting to find in another contemporary fish, the extraordinary form *Dorypterus hoffmanni*, a caudal lobe in precisely the same stage of reduction, except that, in place of the single line of scales found in *Acentrophorus*, the lobe is marked externally to the very tip by two lines, the scales as they are traced backwards becoming linear and almost microscopic. That a stage such as this—the caudal lobe extremely attenuated in its hinder portion but still more or less of the full length—may have been passed through pretty regularly in the production of a "hemi-heterocercal" tail is suggested not only by the parallelism between *Acentrophorus* and *Dorypterus*, but

also by at least one fact of fossil ontogeny. A young example of *Dapedius*, 9 cm. long and beautifully preserved (text-fig. 16), which has been kindly lent me by Prof. D. M. S. Watson, has a caudal lobe extending just two-thirds the length of the upper border of the tail, instead of only one-third as in the adult; and for some distance towards its apex the lobe is marked by a single line of very small and narrow scales.

The head of *Acentrophorus* also, though in side view almost entirely typical of a Semionotid, shows when seen from above (text-fig. 3) some decided primitive traits. The shape of the

Text-figure 16.



Dapedius orbis. Tail of a young example, total length 9 cm., showing extended caudal lobe. Lower Lias; locality uncertain. D. M. S. Watson Collection. About four times natural size.

frontal shield and of the supratemporals, and the large leaf-shaped post-temporals, are all strongly reminiscent of *Palæoniscus*. So also is the internal pattern and articulation of the scales, especially in the earliest species, *A. glaphyrus*.

On the other hand, there are certain points in the structure of *Acentrophorus* which seem to be peculiar to this genus among the Semionotidæ. The orbit is very large and encircled by only a single chain of bones; the scales, compared with those of other Semionotids, are thin, deeply overlapping and of unusual range of difference in size, and do not produce the typical "tessellated

pavement" effect; the fin-fulcra in the later species are of particularly massive form; the pectoral fin is placed higher on the flank than in other fusiform Semionotids, and its attachment gives it a peculiarly "modern" appearance. Fused frontals are also unusual in the family; and of the characters of the axial skeleton which are shown clearly enough to be worth discussion, the expanded neural spines under the dorsal fin and the great size of the supports of the anal fin-rays seem to be quite peculiar to *Acentrophorus*.

In view of all these primitive and individual characters it can no longer be said that *Acentrophorus* differs from *Semionotus* only in lacking the median row of acuminate scales in advance of the dorsal fin. It is seen to be very much the most primitive known member of the family Semionotidæ, and is therefore difficult to incorporate in any scheme on which the genera may be classified. On the whole, however, it would appear to be nearest to the line of ancestry of *Lepidotus*. Such a relationship is suggested in many points, in particular in the shape of most of the fins and in other details of their structure, in the excavation of the back along the base of the dorsal fin, and in the tendency towards a tritoral form exhibited by the teeth on the vomers.

My thanks are due to Prof. D. M. S. Watson, who first suggested the desirability of re-examining the material of *Acentrophorus* in the Hancock Museum at Newcastle; to Mr. J. A. Charlton Deas and Mr. T. R. Goddard for giving me facilities for studying some fine specimens in the Sunderland Museum; and to Dr. W. E. Collinge for similar privileges at York.

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5. The Postorbital Articulation of the Palatoquadrate with the Neurocranium in the Cœlacanthid Fishes. By EDWARD PHELPS ALLIS, Jr., F.Z.S.

[Received October 25, 1922: Read February 6, 1923.]

In a recent work (Allis, 1922), I came to the conclusion that the postorbital articulation of the palatoquadrate with the neurocranium in *Wimania* and *Arelia*, two of the Cœlacanthidæ, was homologous with that in the recent *Hexanchus* and *Heptanchus*, and not with that in *Lepidosteus*. This conclusion was based largely on my assumption that the vena jugularis of these fishes ran posteriorly between the articular process of the palatoquadrate and the cranial wall, instead of accompanying the ramus ophthalmicus lateralis, as suggested by Stensio (1921), and traversing, with that nerve, a foramen that lay between the alisphenoid and basisphenoid bones of the latter author's descriptions. Further consideration of the subject, in connection with a later work by Stensio (1922), has led me to conclude that the vein did not have the course ascribed to it by either Stensio or myself, but, accompanying the ramus ophthalmicus profundus, traversed a foramen that lay anterior, instead of posterior, to the alisphenoid, and so entered a trigemino-facialis chamber in the cranial wall. This conclusion modifies radically my conception of the conditions in these fossil fishes, but I, nevertheless, still think that the articulation of the metapterygoid with the cranium was of the type found in the recent *Hexanchus* and *Heptanchus*, and not of that in *Lepidosteus*.

There are, in recent fishes, two processes of the palatoquadrate that are here concerned, as well as two processes of the neurocranium. One of the processes of the palatoquadrate is the processus basalis, or pedicle, and the other the processus metapterygoideus, and both of them are found in typical condition in the adult *Amia*. The processus basalis of this fish forms the dorso-anterior corner of the metapterygoid, and lies in the plane of the body of the palatoquadrate. It is directed toward the lateral edge of the basis cranii, in the region of the orbital opening of the myodome, and is there connected with it by a band of connective tissue. The floor of the orbital opening of the myodome is the homologue of the processus basiptyergoideus of the Sauria (Allis, 1913), and it is lined ventrally, and supported, by the anterior portion of the ascending process of the parasphenoid. The processus metapterygoideus projects dorso-mesially from the external surface of the metapterygoid, is directed toward the projecting dorso-lateral corner of the postorbital process of the neurocranium, and connected with that process by a membrane that covers the external surface of the

musculus levator arcus palatini (Allis, 1897). It lies between the muscoli levator arcus palatini and adductor mandibulæ, giving insertion, on its internal surface, to certain fibres of the former muscle and origin, on its external surface, to certain fibres of the adductor. It forms the lateral boundary of the surface of insertion of the levator on the palatoquadrate, the mesial boundary of that surface being formed by the processus basalis together with that portion of the dorso-mesial edge of the metapterygoid that lies between that process and the processus metapterygoidæus. That branch of the nervus trigeminus that innervates the levator arcus palatini turns posteriorly around the anterior edge of that muscle, and runs posteriorly on its external surface, thus lying, morphologically, between the processus basalis and the processus metapterygoidæus, dorsal to the one and ventro-mesial to the other. That branch of the external carotid that becomes the secondary afferent pseudobranchial artery (Allis, 1912) has similar relations to these two processes, as has also the vena jugularis. The efferent pseudobranchial artery runs upward and forward ventro-mesial to the processus metapterygoidæus, but its relations to the processus basalis are not positively evident. It lies external to the ascending process of the parasphenoid, and hence would seem to lie morphologically ventral to the processus basipterygoidæus.

In embryos of this fish up to 19.5 mm. in length, the two processes here under consideration are shown by Pehrson (1922, figs. 3-12) apparently both lying on the dorso-mesial edge of the palatoquadrate, the metapterygoid process lying posterior to the basal process and extending farther dorsally in all stages excepting the very earliest. In a 56 mm. specimen, the metapterygoid process has apparently begun to assume its adult position, and the metapterygoid bone has begun to ossify, and it is to be noted that Pehrson shows (*l.c.* fig. 14) the unossified portion of the pterygoquadrate cartilage forming a V-shaped mass, the basalis and metapterygoidæus processes forming the two arms of the V, and the metapterygoid bone lying between them, in the hollow of the V, and not extending upward into either process. The otic process of this fish, and that of the Teleostei as well, is represented in the lateral wall of the trigemino-facialis chamber (Allis, 1914).

The characteristic features of these two processes of this fish thus are: that one of them lies postero-lateral to the other; that the antero-mesial one is directed toward the lateral edge of the floor of the cranium, where the palatoquadrate articulates with it in *Lepidosteus*; that the postero-lateral one is directed toward the lateral edge of the roof of the cranium, where the palatoquadrate articulates with it in *Hexanchus* and *Heptanchus*; that the musculus levator arcus palatini has its insertion on the palatoquadrate between the two processes; that the musculus adductor mandibulæ lies external to the processus metapterygoidæus and is cut off, by it, from any origin or insertion on the

processus basalis; and that the nerve that innervates the levator, the secondary afferent pseudobranchial artery, and the vena jugularis all lie actually, or morphologically, between the two processes.

In *Scomber* (Allis, 1903) and the mail-cheeked fishes (Allis, 1909) these two processes (or flanges developed in relation to them) have acquired contact with the hyomandibula and become firmly attached to it, the processus basalis with its internal surface and the processus metapterygoidens with its external surface. But, notwithstanding this marked difference in the direction of the two processes, and also in their relations to the cranium and the hyomandibula, the levator arcus palatini, the nerve that innervates it, and an artery that corresponds to the secondary afferent pseudobranchial artery of *Amia*, still all lie actually, or morphologically (*Cottus*), between them, and the adductor mandibulæ has its origin on the external surface of the processus metapterygoidens and not at all on the processus basalis. The vena jugularis, also, still lies morphologically between the two processes, for the dorso-mesial edge of the processus basalis is connected, by tissue, with the lateral edge of the basis cranii.

In *Amiurus* the conditions appear, at first sight, markedly different from those in the fishes above referred to, but they are, nevertheless, quite certainly strictly homologous. In a 32 mm. specimen of this fish, Kindred (1919) shows the pterygoquadrate and hyomandibular cartilages completely fused with each other and forming a V-shaped mass with the point of the V directed ventrally. The hyomandibula has begun to ossify on the posterior limb of the V, the metapterygoid on the anterior limb, and the quadrate on the ventrally directed point. Nothing whatever is shown in the hollow of the V, but it must certainly be spanned by membrane, for it is in exactly this place that the metapterygoid bone first appears in *Amia*, as above stated, and in the adult *Amiurus* the corresponding place is occupied by an anteriorly projecting flange of the hyomandibula which sutures anteriorly with the hind edge of the metapterygoid and ventrally with the dorsal edge of the quadrate. Along the dorsal edge of this flange, and of corresponding length, there is a horizontal ridge on the hyomandibula, and the levator arcus palatini is inserted in part on the anterior end of the ridge and in part along the full length of its dorsal surface (McMurrich, 1884). Certain of the deeper fibres of the musculus adductor mandibulæ have their origins on the latero-ventral surface of this ridge, the superficial portion of the muscle extending upward external to the ridge. The anteriorly projecting flange of the hyomandibula of this fish thus corresponds both topographically and functionally to the posteriorly projecting flange on the hind edge of the metapterygoid process of the fishes just above considered, and is quite certainly the homologue of that flange; and that it has become a flange on the anterior edge of the hyomandibula, instead of on

the hind edge of the metapterygoid, is no more extraordinary than the incorporation, in this fish, of the dorsal portion of the preoperculum in the hind edge of the hyomandibula (Kindred, 1919). The metapterygoid, the projecting dorso-mesial portion of which forms the processus basalis, is said to be attached to the lateral surface of the cranium by a sheet of muscular and ligamentous tissue. It is not said at what point on the lateral wall of the cranium this sheet of tissue has its attachment, but two sectional views given through the postorbital region would seem to show that the attachment is either to the trabecula or to the lateral edge of the parasphenoid.

In all of the above-mentioned fishes the palatoquadrate has no direct articular contact with the neurocranium, this articulation being acquired through the intermediation of the hyomandibula, to which the palatoquadrate is firmly fixed. In *Lepidosteus*, *Osteoglossum*, *Hexanchus*, and *Heptanchus* this articulation with the cranium through the intermediation of a hyomandibula still occurs, but in each of them there is, in addition, direct articular contact with the postorbital portion of the cranium; and these are the only recent fishes I know of in which the latter articulation is found, for the palatobasal articulation, found in many of the Selachii, is orbital in position and not postorbital. Gaupp says (1905, p. 767) that an articulation of the palatoquadrate with a processus basiptyergoideus is found in many fishes, but, as he does not mention the particular ones, I have not been able to control the statement. Luther (1913) describes the articulation in *Lepidosteus*, and then says that it is also found in *Osteoglossum* but in no other teleost. It apparently occurs in certain fossil fishes, as in *Boreosomus*, one of the Palæoniscidae described by Stensiö (1921).

In the adult *Lepidosteus*, Parker (1882) describes two processes related to the metapterygoid, one of which he calls the pedicle and the other the otic process. The pedicle is the larger of the two, and is shown forming the dorso-postero-mesial corner of the metapterygoid, the so-called otic process projecting ventro-posteriorly from the ventral edge of the base of the pedicle. The hind end of the pedicle articulates with the anterior edge of a processus basiptyergoideus which projects antero-laterally from the lateral wall of the cranium near its ventral edge, the so-called otic process projecting posteriorly ventral to the processus basiptyergoideus. In a $20\frac{1}{2}$ mm. embryo of this fish, these two processes of the metapterygoid form (Veit, 1911, fig. 17, pl. C.) the dorsal and ventral corners of the actual hind edge of the palatoquadrate, but as this edge of the palatoquadrate of this fish corresponds to the metapterygoid portion of the dorso-mesial edge of the palatoquadrate of *Amia*, the two processes lie, morphologically, one posterior to the other on the posterior portion of the dorso-mesial edge of the palatoquadrate. They accordingly agree exactly, in this, with the basalis and metapterygoid processes of *Amia*, and I shall hereafter so refer to them.

The musculus levator arcus palatini of the adult *Lepidosteus* is said by Luther (1913) to have its origin on the sphenotic, and to run from there antero-mesially to have its insertion on the metapterygoid bone and adjacent portions of the palatoquadrate cartilage. Luther says (*l.c.* p. 13) that: "Dabei umgreift der Muskel das Metapterygoid vor dem Basispterygoid-Gelenk und reicht auch an der Medialseite bis zu etwa $\frac{2}{3}$ der Breite des Knochens hinauf." This would seem to mean that the muscle had its insertion in considerable part on the internal surface of the processus basalis, which would be so unusual for a levator muscle that I have looked it up in transverse sections of an 80 mm. specimen of this fish. In this specimen the muscle, as it approaches the hind end of the palatoquadrate is wrapped around ("umgreift") the lateral edge of the processus basispterygoideus, and when it reaches the hind end of the processus basalis, that part of the muscle that lies ventral to the processus basispterygoideus is inserted on the lateral surface of the processus basalis, this surface of the latter process being presented ventro-laterally. The processus metapterygoides lies against the ventral surface of this part of the muscle, partly imbedded in it, and apparently gives insertion to some of its fibres, but the larger part of the fibres of the muscle continue onward and are inserted on the external surface of the palatoquadrate anterior to the bases of the two processes, none of them being inserted on its internal surface. That part of the adductor muscle that Luther calls the musculus adductor mandibulae postorbitalis lies ventral, and hence external, to the processus metapterygoides, and certain of its fibres have their origins on that process. The action of the levator muscle is said by Luther (*l.c.* p. 61) to be to pull the palatoquadrate almost directly laterally, the motion at the basispterygoid joint accordingly being a sliding one, in a latero-mesial direction, and this is in accord with the position of the long axis of this joint, which is practically at right angles to that of the long axis of the hyomandibulo-cranial articular joint. The nerve that innervates the levator muscle penetrates it from its external surface, and hence lies morphologically between the metapterygoid and basal processes, as it does in the fishes above considered.

The processus basispterygoideus of *Lepidosteus* is said by Parker (1882, pp. 453 & 461) to be developed in part from the trabecula and in part from the parachordal. Veit first (1907) concluded that it is developed from the hind end of the trabecula and corresponds to a part of the floor of the orbit of the Selachii, but he later (1911) says that it arises in connection with the trabecula and the floor of the trigemino-facialis chamber. I first concluded (Allis, 1909) that it is of trabecular origin and, later (1913), that it is the homologue of the floor of the orbital opening of the myodome of *Amia*; but it is to be particularly noted that there is, in *Lepidosteus*, no parasphenoidal leg of the alisphenoid related to the process, as there is in *Amia*, and that there is no membrane that I can recognize replacing it. Veit says that the process

develops late in *Lepidosteus*, and he considers its articulation with the metapterygoid to be a secondary acquisition, and Luther holds the same opinion. The ventral surface of the process, its anterior edge, and the adjacent portions of its dorsal surface are covered and supported by a process of the parasphenoid which would seem to correspond to an anterior portion of the ascending process of the parasphenoid of *Amia*, and it is apparently this process of the bone that alone gives articulation to the metapterygoid in *Osteoglossum*, as explained below. The process of *Lepidosteus* lies ventral to the ramus ophthalmicus profundus and the vena jugularis, and if it be the homologue of the floor of the orbital opening of the myodome of *Amia*, as I concluded, it would seem as if it must lie, morphologically, between the profundus and trigeminus nerves, for its homologue in *Amia* supports the parasphenoidal leg of the alisphenoid, which actually lies between those two nerves. In its relations to these nerves this process thus differs radically from the postorbital process, which always lies, so far as I know, posterior to all branches of the nervus trigeminus, and usually between the foramen for that nerve and the secondary, or definitive, foramen for the nervus facialis. The processus metapterygoides also lies morphologically between the trigeminus and facialis nerves, while the processus basalis, which articulates with the processus basiptyergoides, should have, morphologically, the same relations to those nerves that the processus basiptyergoides has.

In *Osteoglossum* a laterally projecting process of the parasphenoid articulates with a semicylindrical groove on the dorsal edge of an antero-dorsally projecting portion of the metapterygoid (Bridge, 1895), which, as it has exactly the position of the processus basalis of *Amia*, is evidently that process, and when the palatoquadrate swings outward and upward, under the action of the levator arcus palatini, the groove on the metapterygoid has a sliding motion on the process. Posterior to this process, there is a short dorsally projecting process of the metapterygoid which lies against the external surface of the hyomandibula, and hence evidently represents the processus metapterygoides. The laterally projecting process of the parasphenoid has its origin from the base of a pretrigeminus portion of the ascending process of that bone and corresponds to that part of the ascending process of *Lepidosteus* that underlies and supports the basiptyergoid process of that fish, and hence is, functionally, a processus basiptyergoides. It corresponds also to that anterior portion of the ascending process of the parasphenoid of *Amia* that underlies the floor of the orbital opening of the myodome of the latter fish, and the pretrigeminus portion of the ascending process of the parasphenoid of *Osteoglossum* corresponds to one of the two legs of the alisphenoid bone of *Amia*, but which one is uncertain, for the relations of the nerves and the vena jugularis to it are not given.

The conditions in *Heptanchus* and *Hexanchus* I have not

personally examined, but they must be similar to those in *Chlamydoselachus*. In the latter fish the most dorsal portion of the dorso-mesial edge of the palatoquadrate forms the processus metapterygoides, a low ridge on the internal surface of this edge of the apparatus forming the processus basalis (Allis, 1913). In the groove between these two ridge-like processes, the musculus levator maxillæ superioris, which is the homologue of the levator arcus palatini of the Teleostei and Ganoidei, has its insertion, the outer edge of the processus metapterygoides lying between the surface of insertion of the levator muscle and the surface of origin of the adductor mandibulæ. That branch of the nervus trigeminus that innervates the muscle runs posteriorly along its external surface, and hence lies morphologically between the two ridge-like processes. In *Heptanchus* and *Hexanchus* the conditions unquestionably here differ only in that the processus metapterygoides has acquired articular contact with the laterally projecting dorsal portion of the postorbital process, and that, in consequence, the anterior portion of the levator maxillæ superioris runs antero-ventrally beneath the overhanging portion of the postorbital process, and hence internal to the processus metapterygoides. The nerve that innervates this muscle also runs posteriorly internal to the latter process. The levator muscle of these three fishes, and particularly that of *Heptanchus* and *Hexanchus*, can accordingly have but little effect in swinging the palatoquadrate outward and upward, and Luther (1909) says that this motion is impressed upon it by the musculus preorbitalis of his descriptions, which is Vetter's (1874) muscle Add β . This action of this muscle is said to also throw the anterior end of the palatoquadrate downward, the palatobasal (orbital) process sliding downward along its articular contact with the orbital wall. The levator muscle then pulls the palatoquadrate back into place, its action thus being largely, if not entirely, to pull the palatoquadrate dorso-mesially in the plane of the apparatus. The articular attachment of the processus metapterygoides to the postorbital process, in *Heptanchus* and *Hexanchus*, would evidently have to be somewhat loose to permit of this motion, and Luther (1909) assumes that there is here a certain dorso-ventral sliding motion, and, also, that the levator muscle must act in part as an adductor palatoquadrati. Furthermore, the attachment of the palatoquadrate to the hyomandibula must be such as to allow a certain amount of motion between them.

In certain others of the Plagiostomi this metapterygoid ridge of the Notidanidæ has become a pronounced process, and both Gegenbaur (1872) and Luther (1909) have called it a muscle process. It apparently lies directly upon the dorso-mesial edge of the palatoquadrate, thus having in the adults of these fishes the position that it has in larvæ of *Amia*. Where present it has the same relations to the levator and adductor muscles that the ridge-like process of the Notidanidæ has, and because of its articular relations to the cranial wall, in the latter fishes, it has

been quite generally considered to be an otic process; but if, as I have endeavoured to show, it is the homologue of the processus metapterygoideus of the Teleostomi, this cannot be. Goodrich considers it to be an otic process and says (1909, p. 98) that it "appears to have been established very early, since there is reason to believe that it existed not only in the Jurassic *Cestraciontidae* (*Hybodus*), but also in the *Cladoselachii*, *Acanthodii*, and *Pleurocanthodii*."

In certain of the higher vertebrates a pterygo-cranial articulation is found between processes which are apparently the strict homologues either of the processus basalis and basipterygoideus of *Lepidosteus*, or of investing bones related to those processes, the motion between the two processes, however, being a dorso-ventral swinging one instead of a latero-mesial sliding one.

In recent *Amphibia* a cartilaginous processus basipterygoideus seems not to be found (Gaupp, 1900, p. 537), but it is found in certain of the *Stegocephali*, as explained immediately below. The palatoquadrate of the *Amphibia* is said by Gaupp to present four typical processes: a processus oticus, processus ascendens, processus pterygoideus, and processus palatobasalis, the latter process being also called by him (1905, p. 736) simply the processus basalis. In the *Urodela*, the latter process is said to lie, at first, in contact with the ventral surface of the auditory capsule, at the point where the capsule is connected with the basal plate of the skull, and to later there fuse with it. The process is said to seem to correspond to the palatobasal process of the *Selachii*, but this seems improbable, for the processus basalis of the *Amphibia* arises from the pterygoquadrate portion of the palatoquadrate, is directed mesially, and lies against the ventral surface of the floor of the auditory capsule, while the processus palatobasalis of the *Selachii* arises from the palatine portion of the palatoquadrate, is directed dorsally, and lies against the orbital wall, which forms part of the lateral surface of the cranium.

In *Rana*, of the *Anura*, the processus basalis is said by Gaupp (1893, p. 349) to first appear in his fourth stage (young frog about 2 cm. long), there arising from the pars metapterygoidea of the quadrate, close above the root of the processus pterygoideus. It is directed toward the ventral surface of the anterior portion of the auditory capsule, and an articular joint is later there formed, this being considered by Gaupp (1905, p. 737) to be a more primitive condition than the fusion of the process with the auditory capsule in the *Urodela*. In earlier stages of *Rana* there is a processus muscularis rising from the upper edge of the palatoquadrate, strongly developed in the earliest stage described, but gradually diminishing in importance until its complete disappearance during the metamorphosis. This process lies, in larvæ (Gaupp, 1893, p. 292), external to the musculus temporalis and pterygoideus, and gives origin, on its mesial surface, to the masseter, and, on its lateral surface, to the depressor cartilaginis hyoidæ and the depressor mandibulæ. The relations of the

process to the adductor muscles of the mandible are thus not the same as in fishes, but this is probably not important, for the superior and inferior branches of the nervus trigeminus both run forward dorsal or mesial to the process and then turn outward anterior to it. The process lies between the pars articularis quadrati and the processus basalis, in the same relation to those two processes that the processus metapterygoideus of fishes has, and hence is quite certainly the homologue of the latter process. In the Apoda there is said to be no processus basalis (Gaupp, 1905, p. 753).

In the Stegocephali, the palatoquadrate is said to be movable in certain forms, but fixed in by far the larger number. In *Eryops* there is, according to Von Huene (1912), a basiptyergoid process which is apparently a definite process of the basisphenoid bone, but as there is no suture separating the basisphenoid and parasphenoid, the latter bone may also enter into the process. The pterygoid is said to be attached (befestigt sich) to the process by a broad articular surface, the palatoquadrate thus apparently being movable. In *Archegosaurus*, the parasphenoid has, according to Watson (1919), a narrow, outstanding basiptyergoid process on either side, and the pterygoid articulates with it by a freely movable joint; and similar basiptyergoid processes are apparently found in several others of the Rachitomi (*l.c.* p. 53). In *Laccocephalus* the mesial process of the pterygoid suturates with the lateral edge of the parasphenoid in a region that corresponds to that from which the ascending process of the bone of fishes has its origin, and cartilaginous extensions of the basisphenoid are said (*l.c.* p. 54) to "seem to have passed outward above the flat parasphenoid expansions to the epiptyergoid and pterygoid." At the hind end of the suture between the pterygoid and parasphenoid there is a foramen which leads into a canal in the parasphenoid and transmits the internal carotid artery. In *Capitosaurus* the mesial process of the pterygoid suturates both with the parasphenoid and the exoccipital, and there is no basiptyergoid process. The quadrate ramus of the pterygoid is said (Watson, 1919, p. 27) to form "a thin plate, rising nearly vertically, to have a long and close connection with the supratemporal and squamosal. Its upper inner corner has a sutural union with the prootic, with which bone and the supratemporal it forms a large foramen leading forwards over the prootic and epiptyergoid to the anterior part of the skull. This opening must transmit the vena capitis dorsalis and a lymphatic duct. Just above its articulation with the parasphenoid and below the prootic the inner margin of the quadrate ramus of the pterygoid is notched for the passage of the vena capitis lateralis and the seventh nerve." This part of the pterygoid of this amphibian thus has to this part of the skull the topographical relations that the ascending process of the parasphenoid of fishes has, or that the piscine processus metapterygoideus would have if it were to persist and acquire contact with the cranium after the

disappearance of a musculus levator arcus palatini. The processus oticus is part of the epipterygoid bone and lies anterior and internal to this process of the pterygoid.

In the Sauria the processus basalis of fishes must certainly be represented in the meniscus pterygoideus, but whether the processus basalis of recent Amphibia is represented in the meniscus alone, or in that structure together with the processus basipterygoideus, would seem to be an open question. Regarding the development of these structures in the Sauria, Gaupp says (1905, p. 762) that they are both represented, in young embryos of *Lacerta*, by a mass of dense tissue which lies between the foot of the processus ascendens and the root of the trabecula, and is more closely connected with the former than with the latter. When chondrification takes place, this mass separates into two parts, the mesial one chondrifying as a laterally directed process of the trabecula (the processus basipterygoideus) and the lateral one becoming the meniscus. This manner of development of these two structures in this reptile, and their relations to the ascending process of the palatoquadrate, led me to suggest, in an earlier work, that the mass of tissue referred to might represent the pharyngeal element of the mandibular arch.

In the adult *Lacerta*, the meniscus lies on the mesial aspect of the Os pterygoideum (Gaupp, 1905, p. 767), and between it and the processus basipterygoideus an articular joint is formed, the palatoquadrate being movable. In *Sphenodon*, the meniscus and the processus basipterygoideus are also both found (Howes and Swinnerton, 1901), and there is an articular joint between them, as in *Lacerta*, but whether the palatoquadrate of this reptile is movable, or not, I do not find definitely stated. A mesial process of the Os pterygoideum is shown by Fuchs (1901), in an embryo of this reptile, projecting mesially along the ventral surface of the processus basipterygoideus, and it would seem as if it must interfere with any movement, if it does not actually prevent it. Broom (1922) says that Parker described a meniscus, in 1878, in a fairly advanced specimen of *Zootoca*, and he himself describes it in a larval *Agama hispida*, where it lies, as in *Lacerta*, between a cartilaginous processus basipterygoideus and a dermal pterygoid bone. The articular joint is between the meniscus and the processus basipterygoideus, and Broom considers the meniscus to be the homologue of the mesopterygoid of fishes, basing this conclusion on the conditions found in *Eusthenopteron*, a fossil Rhinidistid described by Bryant (1919). The so-called mesopterygoid of the latter fish, as shown in the figure reproduced by Broom, is, however, called by Bryant a metapterygoid, and that part of the bone that has the marked upward extension shown in the latter author's text-fig. 6 would seem to be a processus metapterygoides metapterygoides.

From the above references to the conditions in certain of the Amphibia and Reptilia it is seen that, in these animals, the existing postorbital articulation of the palatoquadrate with the

cranium was primarily, in all probability, that of a processus basalis metapterygoidei with the lateral edge of the basis cranii at or near the hind end of the trabecula. The processus basalis has, in certain of them, later there fused with the basis cranii, while still retaining its connection with the palatoquadrate. In others it has apparently lost its connection with the palatoquadrate but retained that with the neurocranium and then separated into two parts, thus giving rise to a meniscus metapterygoideus and a processus basiptyerygoideus. The metapterygid cartilage is always here lined ventrally, and supported by a dermal pterygoid bone, the processus basiptyerygoideus being similarly lined and supported by a lateral process of the dermal parasphenoid, and in those animals in which the metapterygid and basiptyerygid cartilages are resorbed, or fail to be developed, the two dermal bones replace them and acquire sutural connection with each other.

The conditions in the three Coelacanthidæ so fully and so well described by Stensiö (1921, 1922) may now be considered, and the question is: Is the postorbital articulation of the palatoquadrate of these fishes with the cranium the homologue of that in *Heptanchus* and *Hexanchus*, or of that in *Lepidosteus*, *Osteoglossum*, and higher vertebrates?

The metapterygid of these fishes is a substituent bone, as it is in most recent fishes, and at either end of its dorsal edge there is a pointed process. Between these two processes the dorsal edge of the bone is concave, and articulates with a process of the neurocranium that Stensiö considers to be a processus basiptyerygoideus and which he refers to as the process *e*. In both *Wimania* and *Axelia* this latter process is a process of what Stensiö considers to be a median basisphenoid bone. It is directed dorso-antero-laterally, and in *Wimania* extends so far dorsally that its dorso-anterior corner is shown in contact with the dermal bones of the roof of the skull. In *Axelia* it is shorter, but still extends above the middle line of the lateral surface of the cranium. In *Diplocercoides* it is still shorter, and is a process of a median sphenoid bone and not of a basisphenoid. The metapterygid would seem, from the figures given, to have articulated either with the lateral surface of the process *e* immediately beneath its laterally projecting dorsal edge, or with that edge itself, and as the dorsal edge of the metapterygid is longer than the process *e* is wide, the dorso-anterior end of the metapterygid would seem to have projected anteriorly somewhat beyond the process *e*.

The metapterygid has an even outer surface, without process of any kind, and there is no posteriorly directed process, or other feature, either on this bone or at any place along the hind edge of the palatoquadrate that would indicate a rigid attachment to the hyomandibula. This latter attachment was therefore probably by ligament only, and in this, as also in the general configuration of this part of the palatoquadrate, there is

marked resemblance to the conditions in the Selachii. Stensiö says (1921, p. 73) that there was a large mandibula in *Wimania* (and hence probably in the other two fishes also), and that this presupposes a powerful adductor muscle. Comparison with recent fishes would then indicate that the surface of origin of this muscle on the palatoquadrate must have extended upward at least to the dorsal edge of the metapterygoid, and Stensiö considers it probable that the muscle extended beyond that edge and had its origin in part on the lateral surface of the neurocranium. The levator arcus palatini, if present, would then necessarily have had its insertion, as in *Heptanchus* and *Hexanchus*, either along the dorsal edge of the metapterygoid or partly on that edge and partly on its mesial surface.

On the internal surface of the palatoquadrate there is a large dermal pterygoid bone, and a process of this bone extends to, or nearly to, the point of the dorso-anterior process of the metapterygoid, thus supporting that process. The dorso-posterior process of the metapterygoid, on the contrary, extends considerably beyond the dorsal edge of the pterygoid, this leaving a considerable portion of the internal surface of the metapterygoid exposed beyond the pterygoid. On the lateral surface of the pterygoid there is a strongly pronounced and rounded ridge which extends upward to the point of the dorso-anterior process of the metapterygoid, and strongly suggests that that point represents the dorsal end of some element of the mandibular arch.

The relations of the two processes on the dorsal edge of the metapterygoid to each other, to the palatoquadrate, to the pterygoid, and to the muscles of the arch, thus all strongly suggest that the posterior one is a processus metapterygoideus, and the anterior one either the entire processus basalis or the anterior end of a ridge-like process similar to that in the Selachii, the posterior portion of the ridge lying along the internal surface of the palatoquadrate. There was quite probably a spiracular canal in these fishes, as there is in the recent *Polypterus*, and not simply a diverticulum of that canal, such as is found in the recent *Holostei* and *Teleostei*; and, where this canal is present, there is, in recent fishes, no articulation of the processus basalis with the neurocranium.

There is thus strong presumptive evidence that, in these fishes, it is a processus metapterygoideus that articulates with the cranium, and, in recent fishes, this process never articulates with, or even approaches, a processus basiptyrgoideus. This is evidently in favour of the assumption that the process ϵ is a processus postorbitalis, and the relations to it of the cranial nerves is also in favour of this interpretation.

There is, in *Wimania* and *Axelina*, a median bone which, as already stated, Stensiö considers to be a basisphenoid, and it is said by him to consist of a body (corpus), and three processes on either side, one of these processes being dorsal, one anterior, and

one ventral. The body of the bone is said to be triangular in shape, with the point below, and from there to extend dorso-posteriorly to its thickened base, which is said to lie strikingly high, leaving only a narrow space between it and the roof of the cranium. The bone, as shown in the figures given, has a shape and position which show that it must have occupied, and have completely filled, the hollow of a large cephalic flexure of the brain, both its anterior and its posterior surfaces sloping antero-ventrally. The dorso-posterior edge of the bone is concave, with a short process on either side, and looks like the dorsum sellæ of the skulls of certain vertebrates turned upward and backward. The dorsal process of either side projects dorso-antero-laterally from the corpus, and, in *Wimania*, is, as already stated, so tall that its dorso-anterior corner may be in contact with the postero-lateral corner of the dermosphenotic portion of the fronto-dermosphenotic. The dorsal end of the process thus lies at or near the level of the roof of the cranial cavity, and it is apparently with the ventral surface of the outer end of the process that the metapterygoid articulates. The anterior process of the bone is lamellar in form with its basal portion extending upward along the internal surface of the dorsal process, and it gives support on the dorso-anterior edge of its basal portion to the alisphenoid of Stensiö's descriptions. Dorsal to these two processes the lateral wall of the cranium must have been of cartilage, and this cartilage and the dorsal process must together have formed a laterally projecting dorsal portion of the posterior wall of the orbital fossa, and hence have formed a postorbital process in the sense in which that term is here employed. Stensiö says there is no postorbital process in these fishes, but it is possible that he employs the term in a somewhat different sense. The basisphenoid is traversed, on either side, by but a single canal, which traverses the anterior process and will be later considered.

In *Diplocercides* the anterior portion of the basisphenoid of *Wimania* and *Axelia* is replaced by a sphenoid bone, which extends forward through the orbit to the ethmoidal region and is everywhere in contact, dorsally, with the ventral surface of the dermal bone, or bones, that here form the roof of the cranium. The process *e* of *Wimania* and *Axelia* is, in this fish, apparently simply a protuberance on the lateral surface of the hind edge of the sphenoid, at about the middle of its height. From it a ridge runs upward along the hind edge of the lateral surface of the dorsal half of the sphenoid, and, as it is considered to be the homologue of the alisphenoid bone of *Wimania* and *Axelia*, it is called the alisphenoid wulst. The postclinoid wall of this fish does not project dorsally above the level of the floor of the posterior portion of the cranial cavity, as it does in *Wimania* and *Axelia*.

The truncus maxillo-mandibularis trigemini is considered by Stensiö to have issued from the cranium, in each of the three fishes here under consideration, posterior to the alisphenoid, and

in *Wimania* posterior also to the dorsal process of the basisphenoid. The ramus ophthalmicus profundus of *Axelia* is said to run forward internal to the base of the alisphenoid, and to issue from the cranium anterior to that bone, and in *Diplocercides* it has similar relations to the alisphenoid wulst. In *Wimania* it is said to probably have issued through that small canal, above referred to, that traverses the anterior process of the basisphenoid, but, as will later appear, it is much more probable that this canal was traversed by the efferent pseudobranchial artery. The ramus ophthalmicus lateralis trigemini is said to run forward, in *Wimania*, over the dorsal process of the basisphenoid, close to the lateral wall of the brain-case, thus evidently issuing from the cranium between the dorsal process and the alisphenoid, and then running forward lateral to the latter bone. In *Axelia* this nerve lies in a groove that crosses the external surface of the alisphenoid, and in *Diplocercides* in a canal that traverses the alisphenoid wulst and is continued onward, a certain distance beyond that wulst, in the body of the sphenoid bone. The vena jugularis is said to have had, in *Wimania*, a course similar to that of the ramus ophthalmicus lateralis trigemini. In *Axelia* and *Diplocercides* its course is not given.

The profundus and trigeminus nerves of *Axelia* thus have, in the courses ascribed to them by Stensiö, exactly the relations to the alisphenoid bone of that fish that the corresponding nerves have, in recent fishes, to the parasphenoidal leg (pedicle) of the alisphenoid, the trigeminus nerves all issuing posterior to that leg and the profundus nerve anterior to it; and as the vena jugularis of recent fishes always accompanies the profundus nerve in this part of its course, it seems exceedingly probable that it accompanied that nerve also in *Axelia*, and hence passed, as in recent fishes, antero-mesial to the alisphenoid. In *Diplocercides* the conditions differ from those in *Axelia* only in that the ramus ophthalmicus lateralis trigemini traverses a canal in the alisphenoid part of the sphenoid bone, instead of passing lateral to it; but even in recent fishes, as in *Ania*, this nerve may traverse a foramen that perforates the parasphenoidal leg of the alisphenoid.

In *Wimania* the conditions, as described by Stensiö, differ from those in *Axelia* and *Diplocercides* in that the ramus ophthalmicus profundus is said to have probably traversed the canal in the anterior process of the basisphenoid, that the truncus maxillo-mandibularis trigemini presumably ran outward in a notch at the base of the hind edge of the dorsal process of that bone, and that the vena jugularis accompanied the ramus ophthalmicus lateralis trigemini, and hence passed postero-lateral instead of antero-mesial, to the alisphenoid bone. This course for the latter vein would be most exceptional in fishes, and it seems much more probable that both it and the ramus ophthalmicus profundus passed internal to the alisphenoid, as they both apparently did in

Axelia and *Diplocercides*. The vena jugularis would then continue posteriorly and, having joined the nervus facialis, issue with it through the facialis foramen at the hind edge of the basisphenoid. In this part of its course it must have lain in a canal in the cranial wall, for that it perforated the dura mater and entered the central cranial cavity seems wholly improbable. This canal would thus, in this, exactly resemble the trigemino-facialis chamber of recent fishes, and it seems wholly impossible that the truncus maxillo-mandibularis trigemini did not run forward in it, and issue from it between the process *e* and the alisphenoid. If the truncus issued posterior to the process *e*, as suggested by Stensiö, it would be separated from its ophthalmicus lateralis branch by the entire width of that process, which would be wholly exceptional, as compared with recent fishes, whether the process be a postorbital one or a basipterygoideus. The notch at the base of the hind edge of the process *e* would then probably transmit the ramus palatinus facialis, which is not otherwise accounted for.

If the trigeminus and profundus nerves of *Wimania* and *Axelia* had the courses that I have above ascribed to them, they must have first run upward along the posterior surface of the basisphenoid, then have passed, on either side, lateral to that posteriorly projecting dorsal end of the basisphenoid that resembles a dorsum sellæ, and then have run forward along the dorsal surface of the body of the basisphenoid, there either lying free in the cranial cavity or, much more probably, being enclosed in the canal traversed by the vena jugularis. In recent fishes these nerves run forward across the ventral end of the hollow of the cephalic flexure, instead of upward and forward over it. That part of the basisphenoid bone of *Wimania* and *Axelia* that occupies the hollow of this flexure could not then have arisen from the conditions found in recent fishes by the simple chondrification or ossification of tissues that filled the hollow of the flexure, for the nerves would then have been enclosed, *in situ*, in the cartilage or bone so formed and have traversed canals or foramina in it. And it seems equally improbable that the bone could have grown upward in the hollow of the flexure, pushing the nerves before it. It must then be that, at a certain stage in the development of embryos of *Wimania* and *Axelia*, the anterior end of the notochord was bent upward and slightly backward, as it is in 33 mm. embryos of the recent *Acanthias* (Goodrich, 1918, fig. 14, pl. 2), and that, in the former fishes, this curvature was not later reduced. The cartilago acrochordalis, which, in recent fishes, develops in tissues related to the anterior end of the notochord, was therefore, in *Wimania* and *Axelia*, directed dorso-posteriorly, and its morphologically ventral surface, presented dorso-anteriorly, lay directly beneath the membrane that, in recent fishes, extends from the anterior edge of the cartilago acrochordalis to the top of the preclinoid wall. The hind ends of the trabeculæ, and the bases of the alisphenoid cartilages, would accordingly be carried

upward to the positions the corresponding bones of the adult actually occupy, and that part of each anterior process of the median basisphenoid on which the base of the related alisphenoid rests would correspond to the outer end of the processus basiptyergoideus of *Amia* and *Lacerta*, the remainder of the anterior process apparently corresponding to that little lamellar process that, in *Amia*, forms the lateral wall of the basal portion of the orbital opening of the myodome and is traversed by the foramen for the efferent pseudobranchial artery. There would have been, internal to the alisphenoid, a space traversed by the vena jugularis and the ramus ophthalmicus profundus, the mesial boundary of this space being formed by cartilage that represents the basisphenoidal leg of the alisphenoid. This leg of the alisphenoid would have been continuous, posteriorly, with the mesial wall of a trigemino-facialis chamber, that wall being either of cartilage or of membrane, and the base of the leg of one side of the head would have been connected with that of its fellow of the opposite side by the preclinoid wall. The optic chiasma must have lain upon the dorsal surface of the latter wall, and the lobi inferiores in a depression posterior to it, on the dorsal surface of the membrane (more or less ossified) that covers the dorso-anteriorly presented ventral surface of the cartilago acrochordalis. A median opening in this membrane would lead into a large pituitary sac, which would extend ventrally into the space enclosed between the ventral processes of the basisphenoid, these latter processes thus corresponding to those antero-ventral processes of the parachordals of recent fishes that bound laterally the pituitary fossa. The basisphenoid of these fishes would thus apparently correspond to a bone formed by the fused prootics of recent fishes.

There are thus several features in the cranial anatomy of these fishes that indicate that the so-called dorsal process of the basisphenoid corresponds to some part of the postorbital process of recent fishes, and not to the basiptyergoid process, the most important being that the process gives articulation to a processus metapterygoideus metapterygoidei and not to a processus basalis, that it has no supporting relations to the alisphenoid, and that the truncus maxillo-mandibularis trigemini quite certainly ran outward anterior to it, between it and the alisphenoid. The basisphenoid of these fishes is such a peculiar bone that all comparisons with recent fishes are more or less tentative, and there is one further feature in their cranial anatomy that seems equally peculiar. In all recent bony fishes (Crossopterygii, Holostei, Teleostei) it is, so far as I know, an invariable rule that the dorsal section of the hyomandibular latero-sensory canal runs upward toward, or actually to, a postotic portion of the main infraorbital latero-sensory canal, while in the Plagiostomi this canal turns forward and falls into the infraorbital portion of the main infraorbital canal at the ventro-posterior corner of the orbit. Now, whether correlated to the course of this canal or not, it is a fact that, in all the former fishes the hyomandibula articulates with

the neurocranium dorsal to the vena jugularis, is either traversed by the truncus hyomandibularis facialis or lies anterior to that nerve (*Polypterus*), and is, if I am correct in my conclusions (Allis, 1918), developed from the branchial rays of the hyal arch, while, in the Plagiostomi, the hyomandibula articulates with the neurocranium ventral to the vena jugularis, and is developed either from the pharyngeal or the epal element of the hyal arch (Allis, 1915). In *Polyodon*, where the hyomandibula articulates with the neurocranium dorsal to the vena jugularis, and is of the teleostome type, it nevertheless differs from that in the bony fishes in that it lies posterior to the nervus facialis, and in this fish the hyomandibular canal has a position intermediate between the two above referred to. There may be no morphological significance in this, for there is in certain of the Plagiostomi a line of surface pit-organs that has a position similar to that of the preopercular canal of the bony fishes, and in certain of the latter fishes there are surface lines of pit-organs that correspond in position to that of the hyomandibular canal of the Plagiostomi; but it is to be noted that in the Coelacanthidæ, where a hyomandibula, although presumably present, has not yet been found, the hyomandibular canal has the position of that in the Plagiostomi, while in the Paleoniscidæ, where the hyomandibula was well developed and of the teleostome type, the canal has the position of that in the bony fishes. In the Stegocephali, the canal on the cheek would seem to be formed by the horizontal portion of the canal of the Plagiostomi together with the dorsal portion of the preopercular canal of the bony fishes.

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6. Some Microfilarie found in the Blood of Birds dying in the Zoological Gardens, 1920-1921. By RITA MARKBREITER, B.Sc., Research Assistant in the Helminthological Department of the London School of Tropical Medicine*.

(Text-figures 1-6.)

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From October 1920 till June 1921 the blood of 183 birds which died in the Zoological Gardens of London was examined and 22 were found to contain Microfilarie, roughly 12 per cent. Of these 22 birds, one, a King Bird of Paradise (*Cicinnurus regius*), contained two species of Microfilaria, and these two species each occurred once again separately in other King Birds of Paradise, so that in all 23 Microfilarie of 21 different species were found.

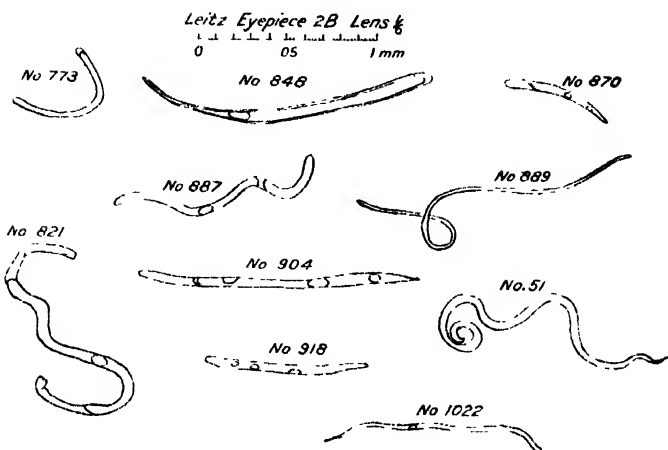
The birds were of 21 species belonging to 15 different families, and came from the following parts of the world:—Mexico, Brazil, S. and N. America, various parts of India, Chili, Java, Madagascar, New Guinea, Malacca, and S. and W. Africa, which shows how wide the distribution of these parasites is. It is not possible to name the embryo parasites unless the adults have been simultaneously found; in these cases they were only found three times, namely:—(1) In the Mexican Hangnest (*Cassidix melanicterus*), the adult being unidentified; (2) in the Occipital Blue-Pie (*Urocissa occipitalis*); and (3) in the Wandering Tree-Pie (*Dendrocitta rayabunda*): in both (2) and (3) the adult was a Diplotriæna, and it is interesting to note that the corresponding Microfilarie are of the same type though they differ in size.

As in the Microfilarie of man, the avian Microfilarie fall into two distinct types, sheathed and unsheathed, and in both groups many different forms are found, long and short, thick and thin, coiled and straight. Three of the Microfilarie listed were also found by Plimmer, namely, the short form, occurring in *Cicinnurus regius*, and those in *Urocissa occipitalis* and *Cittocincla macrura*; the others are reported for the first time. In the detailed lists which are appended the adjectives short, medium length, long and thin, medium thickness, and thick are represented by the following measurements:—Short = 0-100 μ ; thin = under 3 μ ; medium length = 100-200 μ ; medium thickness = 3-4 μ ; long = over 200 μ ; thick = over 4 μ .

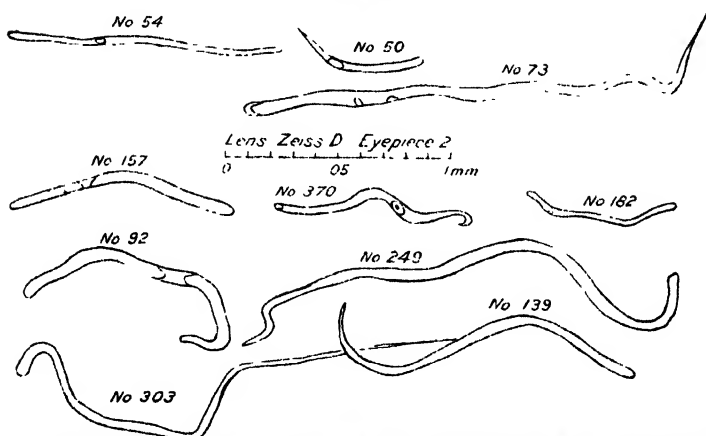
Reference.—Plimmer, "On the Blood Parasites found in Animals in the Zoological Gardens," Proc. Zool. Soc., 1912.

* Communicated by Prof. R. T. LEIPER, M.D., D.Sc., F.Z.S.

Text-figure 1.



Text-figure 2.



Outlines of Microfilaria to show comparative sizes and forms. Camera lucida used. Leitz microscope: eyepiece 2B; lens $\frac{1}{2}$ for drawings 773 (1920) to 1022 (1920) and 50 (1921) to 73 (1921).

Zeiss microscope: eyepiece 2; lens ZD used for drawings 92 (1921) to 370 (1921).

The numbers referring to Microfilaria in text-figs. 1 and 2 are those of the Death Book of the Zoological Society for the years 1920 and 1921.

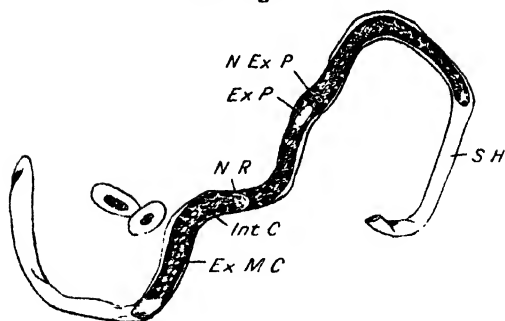
TEXT-FIG. 1.

773. Host. *Cassidix melanicterus*.
 821. " *Irene turroa*.
 848. " *Cacoabis chukar*.
 889. " *Cicinnurus regius*.
 887. " *Psittinus incertus*.
 870. " *Cicinnurus regius*.
 904. " *Urocissa occipitalis*.
 918. " *Dendrocitta vagabunda*.
 1022. " *Agapornis cana*.
 51. " *Hypochaeris nitens*.

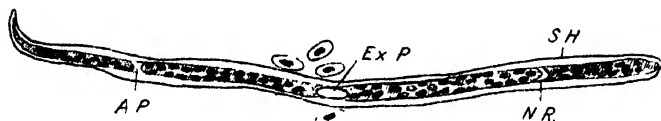
TEXT-FIG. 2.

54. Host. *Serinus scotops*.
 50. " *Quiscalus quisqualis*.
 73. " *Bubulcus coromandus*.
 92. " *Ottagyps calvus*.
 139. " *Elanus caeruleus*.
 157. " *Paradisaea minor*.
 182. " *Turdus corythae*.
 249. " *Steganura paradisaea*.
 303. " *Oittocincla macrura*.
 370. " *Ramphocelus brasilis*.

Text-figure 3.



Text-figure 4.



Text-figure 5.



Text-figure 6.



Freehand drawings to show details.

Text-fig. 3. *Microfilaria* out of *Irene turroza* (Fairy Blue-Bird).

" 4. *Microfilaria* out of *Caccabis chukar* (Chukar Partridge).

" 5. *Microfilaria* out of *Cicinnurus regius* (King Bird of Paradise).

" 6. *Microfilaria* out of *Cicinnurus regius* (King Bird of Paradise).

Ex.P. = excretory pore. N.Ex.P. = nucleolus of excretory pore. Ex.M.C. = external muscle cells. Int.C. = internal cells. G.R. = genital region. N.R. = nerve ring. S. = sheath.

Host.	Habitat.	Admission to Gardens.	Helminth.
ICTERIDÆ. <i>Cassidix melanicterus</i> (Mexican Hang- nest).	Mexico	9. 6. 20	Microfilaria. Sheathed, short, medium thickness, blunt tail, no cells at one end of the body. Adult found by Dr. VEVERS. Length with sheath . . . 86 μ 84 86 Length with- out sheath 84 82 82 Breadth . . . 4 4 4
TURDIDÆ. <i>Irene turroa</i> (Fairy Blue-Bird).	Java	13. 10. 20	Microfilaria. Sheathed, long with sheath, body of medium length; thick, graceful. Blunt tail; cells in end of tail. Length with sheath . . . 267 μ 214 198 Length with- out sheath 162 133 119 Breadth . . . 8 8 7
PHASIANIDÆ. <i>Caccabis chukar</i> (Chukar Part- ridge).	N.W. India	16. 7. 23	Microfilaria. Sheathed, medium length, thick. Pointed tail; cells to end of tail. Length with sheath . . . 168 μ 176 93 Length with- out sheath . . . 164 174 92 Breadth with sheath . . . 7 8 6 Breadth with- out sheath . . . 5 6 4
PARADISEIDÆ. <i>Cicinnurus regius</i> (King Bird of Paradise).	New Guinea	13. 10. 20	Microfilaria. Unsheathed, short, medium thickness. Pointed tail, nearly straight. Length . . . 61 μ 61 73 Breadth . . . 4 4 4
PSITTACIDÆ. <i>Psittinus incertus</i> (Blue-rumped Parrakeet).	Malacca	13. 10. 20	Microfilaria. Unsheathed, medium length and thickness. Length . . . 130 μ 170 148 Breadth . . . 4 4 4
PARADISEIDÆ. <i>Cicinnurus regius</i> (King Bird of Paradise).	New Guinea	13. 10. 20	Microfilaria as in previous King Bird of Paradise. Length . . . 60 μ 60 62 Breadth . . . 4 4 5 Also Microfilaria, long and slender, with pointed end. Unsheathed. Length . . . 218 μ 220 Breadth . . . 1.5 2
CORVIDÆ. <i>Urocissa occipitalis</i> (Occipital Blue- Pie).	Himalayas	16. 7. 20	Microfilaria (a <i>Diplotriana</i> sp., adult found by Dr. VEVERS). Unsheathed, medium length, and thick. Pointed, tilted tail. Length . . . 143 μ 158 150 Breadth . . . 4-5 4-5 4-5
CORVIDÆ. <i>Dendrocitta vagabunda</i> (Wandering Tree- Pie).	India	4. 6. 20	Microfilaria (a <i>Diplotriana</i> sp., adults found by Dr. VEVERS). Unsheathed, short, thick. Pointed tail. Similar in type to preceding microfilaria. Length . . . 90 μ 100 90 Breadth . . . 5 4 4

<i>Host.</i>	<i>Habitat.</i>	<i>Admission to Gardens.</i>	<i>Helminth.</i>
PSITTACIDÆ. <i>Agapornis cana</i> (Love-Bird).	Madagascar	24. 9. 17	Microfilaria. Unsheathed, medium length, thin. Pointed tail. Length 128 μ 124 130 Breadth . . . 2 2-3 3
PARADISEIDÆ. <i>Cicinnurus regius</i> (King Bird of Paradise).	New Guinea	13. 8. 20	Microfilaria. Unsheathed, medium length to long, thin, pointed at one end. Length 198 μ 184 205 Breadth . . . 2 2 2
PLOCEIDÆ. <i>Hypochera nitens</i> (Shining Weaver-Bird).	W. Africa	8. 9. 19	Microfilaria. Unsheathed, long, thick, pointed at one end, blunt end coiled. Length 304 μ 250 Breadth . . . 5-6 5
FRINGILLIDÆ. <i>Serinus scotops</i> (Seed-eater).	S. Africa	21. 1. 21	Microfilaria. Unsheathed, medium length and thickness, one end pointed. Length . . . 150 μ 128 104 Breadth . . . 4 4 4
ICTERIDÆ. <i>Quiscalus quisicalus</i> (Purple Grackle).	N. America	9. 6. 20	Microfilaria. Unsheathed, short, medium thickness, one end pointed Length .. 78 μ 78 78 76 86 Breadth . . 3-4 3 4 3-4 3-4 3-4
ARDEIDÆ. <i>Butor coromandus</i> (Cattle Egret).	India	28. 4. 20	Microfilaria. Unsheathed, long and thick, end tilted and very pointed. Length . . . 237 μ 308 337 Breadth . . 6-7 6-7 6 7
VULTURIDÆ. <i>Otopsis calvus</i> (Pondicherry Vulture).	"	16. 7. 20	Microfilaria. Unsheathed, thick, medium length, slightly pointed at one end. Length .. 140 μ Breadth . . 8
FALCONIDÆ. <i>Elanus caeruleus</i> (Black-shouldered Kite).	W. Africa	3. 5. 20	Microfilaria. Unsheathed, medium length and breadth. Length . . . 200 μ 162 180 152 Breadth . . 3 3-5 4 2-5
PARADISEIDÆ. <i>Paradisaea minor</i> (Minor Bird of Paradise).	New Guinea	27. 10. 19	Microfilaria. Unsheathed, short, medium thickness, nearly straight, ends blunt. Length .. 100 μ Breadth 4
MUSOPHAGIDÆ. <i>Turacus corythax</i> (Touraco).	S. America	29. 9. 20	Microfilaria. Unsheathed, short, thin. Length . . . 72 μ Breadth 2
COLUMBIDÆ. <i>Zenaidura auriculata</i> (Auriculated Dove).	Chili	24. 8. 17	One microfilaria, partially hidden by corpuscles and badly seen, medium length and thickness. Length 180 μ Breadth 4
PARADISEIDÆ. <i>Steganura paradisaea</i> (Paradise Whydah-Bird).	W. Africa	7. 7. 19	Microfilaria. Unsheathed, long and thick, blunt one end, pointed the other. Length 315 μ 260 245 Breadth 5 5 6

<i>Host.</i>	<i>Habitat.</i>	<i>Admission to Gardens.</i>	<i>Helminth.</i>
TURDIDÆ. <i>Cittocincla macrura</i> (Shama).	India	16. 7. 20	Microfilaria. Unsheathed, long. graceful, thick and blunt at the anterior end, tapering gradually to a slender pointed posterior end. Length 230 μ 244 244 Thickest breadth 5 5 5
TANAGRIDÆ. <i>Ramphocelus brasilius</i> (Scarlet Tanager).	Brazil	18. 12. 19	Microfilaria. Unsheathed, graceful, blunt at one end which contains a clear refractory body; other end pointed and frequently curled, medium length and thickness. Length 120 μ 100 90 Breadth 6 6 5.5

7. On the Vagus and Sympathetic Nerves of the Terrestrial Carnivora. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received October 2, 1922: Read February 6, 1923.]

(Text-figures 1-14.)

The course, relations, and branches of the vagus and sympathetic nerves in the dog and cat are described in text-books, and Swan (1) has recorded some of the conditions present in the fox, jaguar, and porpoise. But no account of these nerves in the entire group of terrestrial Carnivora has been published. In the present paper, which is based on the examination of animals which died in the Society's Gardens, the conditions present in representatives of all families except the Hyænidæ, Protelidæ and Cryptoproctidæ, are described. The course and relations in all forms resemble those in the dog and cat.

The cervical parts of the vagus and sympathetic nerves may be fused or separate, or both forms may be present in the neck of the same animal.

The cervical parts are fused in :—

Family Felidæ:—*Felis domestica*, *F. onca*, *F. sylvestris*, *F. bengalensis*; Family Viverridæ:—*Nandinia binotata*, *Viverra civetta*, *Civettictis civetta*, *Viverricula malaccensis*, *Paradoxurus larvatus*, *Mungos mungo*, *M. ichneumon*, *Atilax paludinosus*, *Cynictis penicillata*; Family Canidæ:—*Canis familiaris*, *C. thous*, *C. bengalensis*, *Vulpes vulpes*, *Lycan pictus*; Family Mustelidæ:—*Mustela martes*, *Meles meles*, *Putorius vison*, *Mephitis mephitis*, *Ichtonyx zorrilla*; Family Procyonidæ:—*Procyon lotor*, *Nasua narica*; Family Ursidæ:—*Melursus ursinus*. The degree of fusion varies. It may consist of an intimate mingling of the fibres, or the nerves may be easily separated when the fused sheaths are divided. The fusion may occur low down or high up. It is most extensive in *Nandinia binotata*, in which the ganglion nodosum of the vagus, and the superior cervical ganglion of the sympathetic are fused to form a lobulated mass (text-fig. 1 A). The vagus and inferior cervical ganglion are fused in *Canis thous* (text-fig. 5), *Paradoxurus larvatus* (text-fig. 6), and *Civettictis civetta* (text-fig. 7 B). The cervical parts are separate in *Genetta felina*, *Paradoxurus hermaphroditus*, and *Ailurus fulgens*. Both forms are present in the same animal in a specimen of *Lutra maculicollis*, the nerves being fused on the left side and separate on the right*.

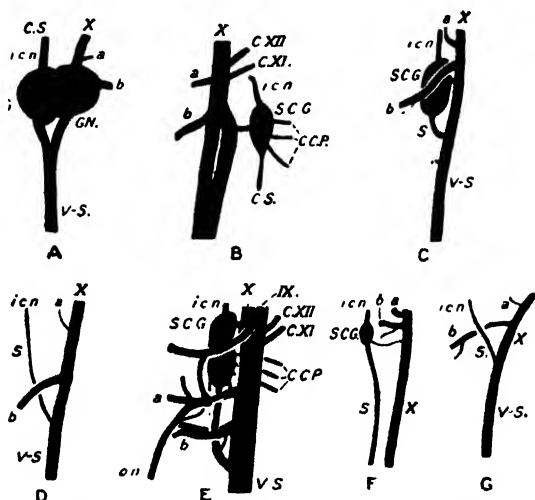
* A similar condition has already been recorded in *Tamandua tetradactyla* (4) and in *Anthropopithecus troglodytes*.

The Vagus Nerves.

The *ganglion nodosum* is absent in *Ailurus fulgens*, *Ictonyx zorilla*, *Paradoxurus larvatus*, *Melursus ursinus*, *Atilax paludinosus* and *Genetta felina* (text-fig. 1 B-G). It is represented by a thin, flat, expanded part of the nerve in *Civettictis civetta*, *Mustela martes*, *Meles meles*, and *Mephitis mephitis* (text-fig. 2); and in other genera it is a well-marked, round, oval, fusiform or pyriform swelling (text-fig. 3). Communications run as usual between it and the other nerves in its vicinity.

The *vago-sympathetic cord* (text-figs. 1, V-S.-11, V-S.) usually

Text-figure 1.



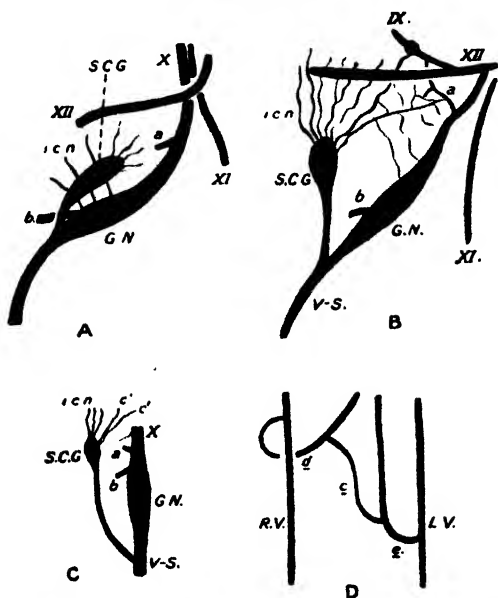
The upper cervical parts of the vagus and sympathetic nerves in: A. *Nandinia binotata*; B. *Ailurus fulgens*; C. *Paradoxurus larvatus*; D. *Atilax paludinosus*; E. *Melursus ursinus*; F. *Genetta felina*; G. *Ictonyx zorilla*; C.S: cervical sympathetic; X: vagus nerve; IX: glossopharyngeal nerve; XII: hypoglossal nerve; G.N: ganglion nodosum; S.C.G: superior cervical ganglion; V-S: vago-sympathetic; C.C.P: communications to cervical plexus; a: pharyngeal nerve; b: internal laryngeal nerve; i.c.n: internal carotid nerve.

separates again into vagus (V.) and sympathetic (S.) in the posterior third of the neck, but they separate in the anterior part of the thorax in *Canis thous* (text-fig. 5). I believe the large swelling seen on the nerve in that species is a fusion of the vagus and inferior cervical sympathetic ganglion. It represents a greater degree of fusion than that seen in text-figs. 6 and 7 B.

Pharyngeal Nerve (text-figs. 1 a, 2 a, 3 a):—This nerve arises from the ganglion nodosum or from the nerve above it, the latter

being more frequent; and it runs to the pharyngeal plexus where it meets branches of the spinal accessory and sympathetic nerves. The accessory filaments usually pass through the vagus, but in *Canis familiaris* (1) they run separately. In *Mungos ichneumon* (text-fig. 3 B) the pharyngeal nerve is given off from a laryngeal nerve. In *Procyon lotor* (text-fig. 3 D) the pharyngeal nerve communicates with the superior laryngeal nerve; and in *Mustela martes* (text-fig. 2 B) and *Civettictis civetta* (text-fig. 2 A) the sympathetic communicates with it before it reaches the pharyngeal plexus.

Text-figure 2.



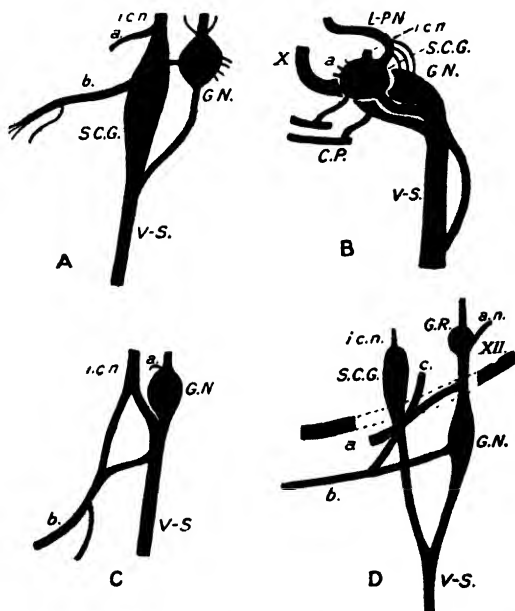
The upper cervical parts of the vagus and sympathetic nerves in: A. *Civettictis civetta*; B. *Mustela martes*; C. *Meles meles*; D. Anastomoses between the recurrent nerves in *Meles meles*: L.V. and R.V.: left and right vagi; d. and e.: right and left recurrent nerves; c: communicating nerves. Other letters as in text-fig. 1.

The superior laryngeal nerve (text-figs. 1 b, 2 b, 3 b) is the largest branch given off from the ganglion nodosum, or from the upper part of the vagus when no ganglion is present. In *Mungos ichneumon* (text-fig. 3 B) the superior cervical ganglion of the sympathetic gives off a large nerve (L-P-N.) which receives three filaments from the ganglion nodosum, and supplies the pharynx and larynx. The superior cervical ganglion, or sympathetic cord, communicates in some cases with the superior laryngeal nerve by small branches, or by a thick cord, as in *Canis thous*

(text-fig. 3C). The nerve gives off the external laryngeal nerve and enters the larynx through the thyro-hyoid membrane, or through an opening in the thyroid cartilage. It is sometimes seen to communicate with the recurrent nerve, but never in such a complete manner as that described in *Hyrax capensis* (5). No trace of a depressor nerve was seen in any of the animals described in the present paper, although it is described by several authors as existing in *Felis domestica*.

As the middle cervical sympathetic ganglion is absent, no

Text-figure 3.



The upper cervical parts of the vagus and sympathetic nerves in: A. *Felis bengalensis*; B. *Mungos ichneumon*; C. *Canis thous*; D. *Procyon lotor*; G.R: root ganglion of the vagus; a.n: Arnold's nerve. Other letters as in text-fig. 1.

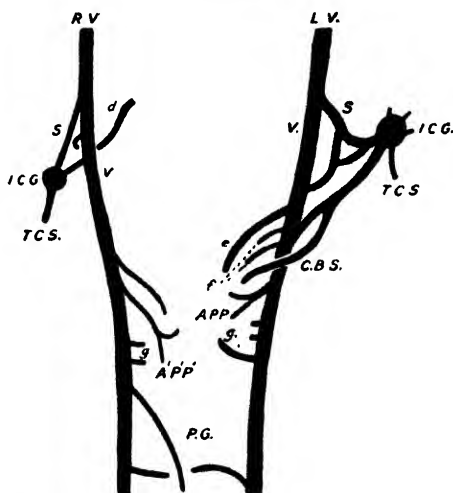
communicating twigs are given off from the vagus till the root of the neck is reached. There the sympathetic is given off and communicating branches run again between vagus and sympathetic. They run to the sympathetic cord itself, or to the inferior cervical ganglion of the sympathetic (text-figs. 4-11). In *Procyon lotor* they run from the vagus to the annulus of Vieussens.

The cervical part of the oesophagus is supplied by the pharyngeal and, in some cases, the recurrent laryngeal nerves.

The *right recurrent laryngeal nerve* (text-figs. 4, d-11, d) has the usual origin, course, and relations. It may communicate with the sympathetic and cardiac plexuses. In *Meles meles* (text-fig. 2 D) a thick nerve unites it to the left recurrent nerve, and in *Mephitis mephitis* (text-fig. 11 A) it forms a loop with the right vagus, whence cardiac branches arise.

The left vagus usually runs straight across the aortic arch, but in *Canis thous* (text-fig. 5) it is very tortuous, and its branches are also undulating, so the aortic arch is covered by sinuous nerves.

Text-figure 4.



The lower cervical and thoracic parts of the vagus nerves in *Felis bengalensis*.

L.V. and R.V.: left and right vago-sympathetic nerves; V: vagi; S: sympathetics, A.P.P. and A'.P'.P': anterior pulmonary plexuses; C.B.S.: cardiac branches of the sympathetic; I.C.G.: inferior cervical ganglion of the sympathetic; P.G.: plexus gule; T.C.S.: thoracic sympathetic cords; d and e: right and left recurrent laryngeal nerves; f: cardiac branches of the vagus; g and g': pulmonary branches of the vagus.

The *left recurrent laryngeal nerve* (text-figs. 4, e-11, e) arises from any point in the vagus above, in front of, or below the aortic arch. It has the usual course, relations, and terminations. It gives twigs to the cardiac plexus, and it may communicate with the left anterior pulmonary plexus.

Tracheal and œsophageal branches arise in the thorax, and the former make a more or less complex plexus.

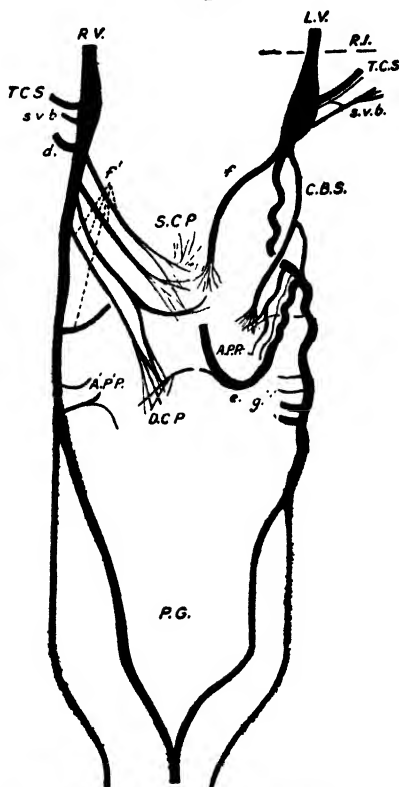
Cardiac Nerves (text-figs. 4, f, f'-11, f, f'):—In none of the terrestrial Carnivora did I observe any cervical cardiac branches

of either vagus; and all the branches arose within the thorax from:—

- a. The vagus nerves (constant).
- b. The left recurrent nerve (constant).
- c. The right recurrent nerve (not universal).

In all forms the vagus cardiac branches contain some sympathetic filaments, but in a few species they contain the entire

Text-figure 5.



The thoracic parts of the vagus nerves in *Canis thous*. D.C.P. and S.C.P.: deep and superficial cardiac plexuses; R.I.: first rib; s.v.b.: sympathetic nerves on subclavian arteries. Other letters as in text-fig. 4.

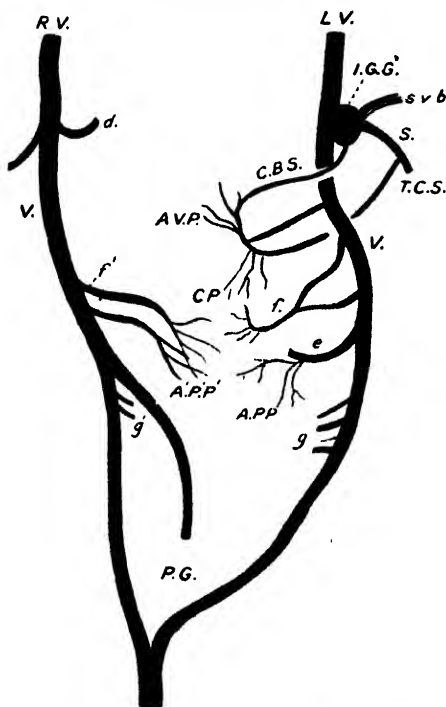
sympathetic supply to the heart. The cardiac plexuses anastomose with the anterior pulmonary plexuses, and with the nerves round the branches of the aortic arch. In some cases (text-figs. 4, 5, 6) the vagus gives off well-marked nerves, whose bifurcating terminal twigs run to both cardiac and anterior pulmonary nerves. The actual components of the plexuses are described on p. 76.

Anterior Pulmonary Nerves (text-figs. 4, A.P.P.-11, A'.P'.P'.) arise from the vagi anterior to the pulmonary roots, or as bifurcations from cardio-pulmonary branches.

Posterior Pulmonary Nerves (text-figs. 4, g.g.-11, g.g'.), which are two to four in number, arise from the vagi as they run along the dorsal surfaces of the roots of the lungs. They may be very short and minute, or long and thick.

Plexus Gulae (text-figs. 4-11):—Between the roots of the lungs and the diaphragm there is a more or less intricate anastomosis between the vagi across the oesophagus. There may be only

Text-figure 6. *



The lower cervical and thoracic parts of the vagus nerves in *Paradoxurus larvatus*. s.v.b: sympathetic nerves on the subclavian arteries. Other letters as in text-fig. 4.

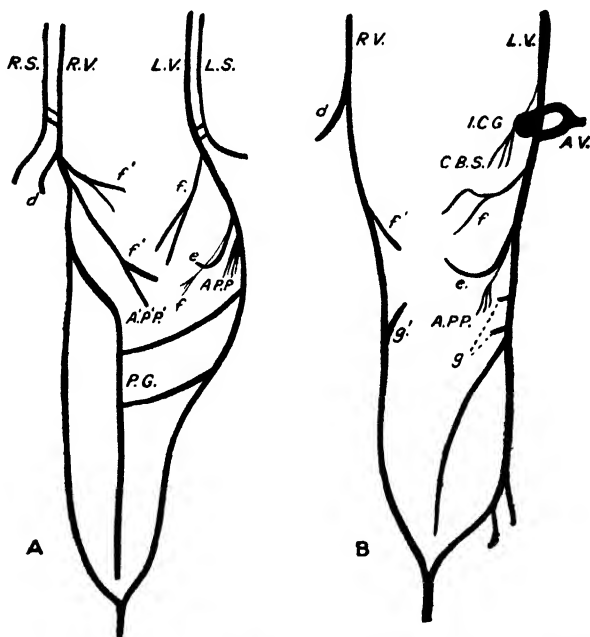
branches of communication, but in most forms there is a mingling of divisions of the vagi. From the plexus two cords emerge; one runs through the ventral aspect of the oesophageal orifice in the diaphragm and the other through its dorsal aspect. The arrangements observed by me were:—

In *Nandinia binotata*, *Mephitis mephitis* (text-fig. 11 A),

Oynictis penicillata (text-fig. 10 B), and *Melursus ursinus* (text-fig. 11 B) the ventral cord is formed by the left vagus, the dorsal cord by the right one, and communications run between the nerves.

In *Felis bengalensis* (text-fig. 4) and *Paradoxurus larvatus* (text-fig. 6) the ventral cord is a branch of the right vagus and the dorsal cord is a combined trunk of the vagi. In the former communications run between the vagi. In *Genetta felina* (text-fig. 7) the ventral cord and left vagus are united by communications.

Text-figure 7.



The thoracic parts of the vagus nerves in: A. *Genetta felina*; B. *Civettictis civetta*. Letters as in text-fig. 4.

In *Civettictis civetta* (text-fig. 7 B), *Ailurus fulgens* (text-fig. 10 A), *Lutra maculicollis* (text-fig. 8 A), and *Putorius vison* (text-fig. 8 B) the dorsal cord is a combined trunk of the vagi, and the ventral cord is a branch of the left vagus.

In *Procyon lotor* (text-fig. 9 B) the ventral and dorsal cords are produced by both vagi after forming a complex plexus gulæ.

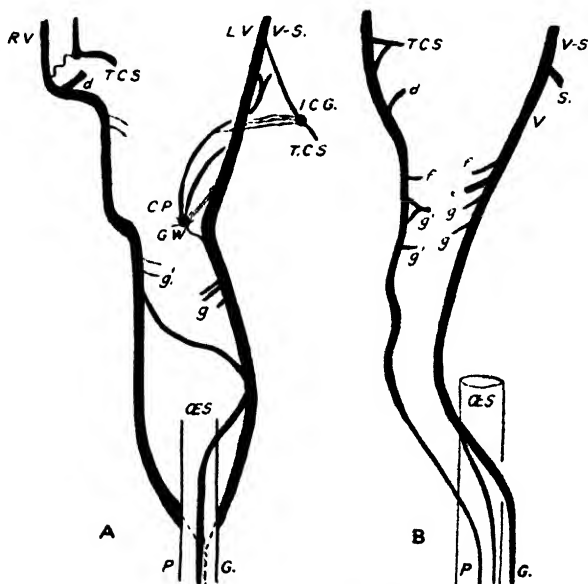
In *Canis thous* (text-fig. 5) both vagi divide. The mesial halves unite to form the ventral cord, and the lateral halves fuse to form a very thick dorsal cord.

The ventral and dorsal cords end in different ways in the

abdomen. In *Felis bengalensis* (text-fig. 12) the ventral cord sends branches over the ventral gastric wall and lesser curvature. They anastomose with branches of the right vagus and off-shoots of the solar plexus accompanying the gastric and duodenal arteries. The right vagus supplies dorsal gastric nerves and divides into two bundles of fibres which end in the celiac ganglia (O.G.), gastric (G.P.), splenic (S.P.), superior mesenteric (S.M.P.), and left renal (L.R.P.) plexuses.

In *Civettictis civetta*, *Atilax paludinosus*, *Genetta felina*, *Ictonyx zorrilla*, *Mephitis mephitis*, *Melurus ursinus*, and *Ailurus fulgens* the ventral cord divides into branches which supply the ventral

Text-figure 8.



The thoracic parts of the vagus nerves in: A. *Lutra maculicollis*; B. *Putorius vison*; G.W.: ganglion of Wrisberg; ES: œsophagus. Other letters as in text-fig. 4.

surface of the stomach and course along the lesser curvature to the pylorus. The dorsal cord sends a few branches to the lesser curvature and dorsal wall of the stomach and ends in the solar plexus; it always remains large and thick.

In *Paradoxurus larvatus* (text-fig. 13) the conditions are very complex. The ventral cord (V.C.) supplies the stomach, as in the preceding forms, by thin gastric branches (*g.b.*), but it also gives off the hepatic plexus (H.P.). The dorsal cord (D.C.) gives off a large gastric nerve (G.P.), several twigs to the hepatic plexus (H.P.), the splenic plexus (S.P.), and many communicating

branches to the solar plexus (c.S.P.). It is continued into the superior mesenteric plexus (S.M.P.), one branch in particular being thick and reaching the cæcum (Ca). These sympathetic plexuses even if traversing the vagus cord have come from the solar plexus.

In *Canis thous* the ventral cord runs along the lesser curvature of the stomach to the pylorus, but it does not give off the hepatic plexus. The dorsal cord supplies the dorsum of the stomach, communicates with the solar plexus by a large cord, and sends many branches into the solar offshoots. Many branches can be traced through the superior mesenteric plexus to the cæcum.

In *Cynictis penicillata* the right vagus replaces the ventral cord in the species described above, but has a similar course. The left one runs through the dorsal aspect of the œsophageal opening in the diaphragm, supplies the stomach, and breaks up into filaments which pass to the offshoots of the solar plexus.

It is now believed that the Arctoid Carnivora have genetic relations to the Cetacea, and Swan (1) described the conditions in *Phocæna communis* as follows:—"In the porpoise the par vagum communicates with the sympathetic, but is otherwise separate from this, as in the baboon, rabbit, and others; it gives off a small recurrent which winds round the subclavian artery on the right side, and the arch of the aorta on the left; it sends filaments to the œsophagus; it gives several branches to the heart, and copiously supplies the lungs; it then passes to the œsophagus, where its branches are more deeply imbedded in the muscular fibres than in other animals; the greater portion corresponding with the posterior trunk supplies the first, or cuticular, and the second, or villous, stomach; after forming a corona or ring on the lower part of the œsophagus, it sends filaments to the diaphragm and to the left semilunar ganglion; it also sends branches towards the other three stomachs or duodenal pouches, a branch to the liver, and others to communicate with branches from the celiac plexus on the branches of the coronary artery passing to the stomachs, and with some of the branches of the hepatic plexus as this passes to the liver; the smaller portion corresponding with the anterior trunk passes down and sends some filaments to the lower portion of the œsophagus and the first stomach, but its principal part divides to join both semilunar ganglia."

It is, therefore, evident that there is a greater degree of communication between the vagi and solar plexus in the porpoise than in the Arctoid Carnivora, both trunks being connected to the semilunar ganglia. Complications are introduced owing to the differences in the characters of the stomach.

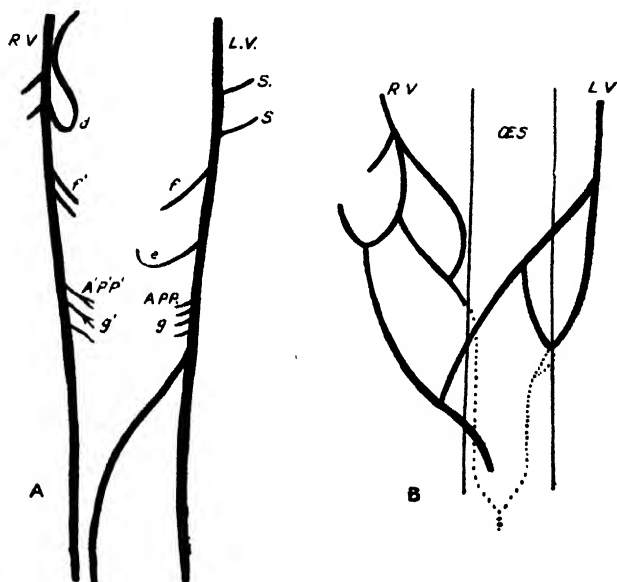
The Sympathetic Nervous System.

The superior cervical ganglion (text-figs. 1, S.O.G.-3, S.O.G.) is absent in *Atilax paludinosus*, *Ictonyx zorrilla*, and *Canis thous*,

and I could neither observe it in the neck nor in the carotid canal. In other species it is round, oval, or pyriform, but its posterior pole is never bifurcated. It communicates with the ninth, tenth, and twelfth cranial nerves, and it sends branches to the pharyngeal plexus. The internal carotid nerve (i.c.n.) is single or multiple. Rami communicantes also run to the upper cervical spinal nerves.

The superior cervical ganglion and ganglion nodosum are fused in *Nandinia binotata* (text-fig. 1 A), but in other animals the former rests on the vagus nerve, or is connected to it by a sympathetic cord (S.) of variable length. In only a few species (p. 65) is the sympathetic always separate from the vagus.

Text-figure 9.



A. Thoracic parts of the vagus nerves in *Ictonyx sorilla*; B. Plexus gularis in *Procyon lotor*. Letters as in text-fig. 4.

In no case is there a *middle cervical ganglion*.

When a vago-sympathetic cord is present it is usually resolved again into its component elements in the posterior third of the neck. But in *Canis thous* (text-fig. 5) the vago-sympathetic passes into the thorax, and expands into an oval mass whence the sympathetic runs cranio-laterad. The sympathetic enters the inferior cervical ganglion or the first dorsal ganglion when the former is absent.

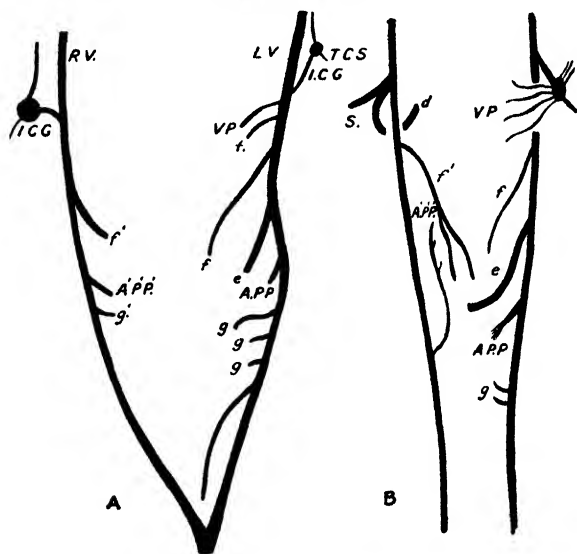
The *inferior cervical ganglion* (text-figs. 4, I.C.G.-11, I.C.G.) is absent in *Putorius vison*, *Atilax paludinosus*, *Genetta felina*, and

it is, in my opinion, represented by the swelling on the vagus in *Canis thous* (text-fig. 5). In *Civettictis civetta* (text-fig. 7 B) it is fused with the medial border of the left vagus, but it is absent on the right side. It may communicate with the right recurrent nerve. Branches run to the brachial plexus, and vaso-motor filaments accompany the vessels to the fore-limbs.

In *Canis thous* (text-fig. 5, s.v.b.) the latter arise independently from the vagus enlargement. Branches accompany the vertebral artery through the cervical vertebrae.

Cardiac branches reach the cardiac plexuses in three ways. In most species they are contained within branches of the vagus.

Text-figure 10.



Thoracic parts of the vagus nerves in : A. *Ailurus fulgens*; B. *Cynictis penicillata*; V.P. : nerve plexus round branches of the aortic arch. Other letters as in text-fig. 4.

In some forms they reach the cardiac plexuses through the plexus round the aortic arch and its branches. In others they run directly to the cardiac plexuses.

The inferior cervical ganglion is united to the first thoracic ganglion by one or more nerves, or by an annulus of Vieussens.

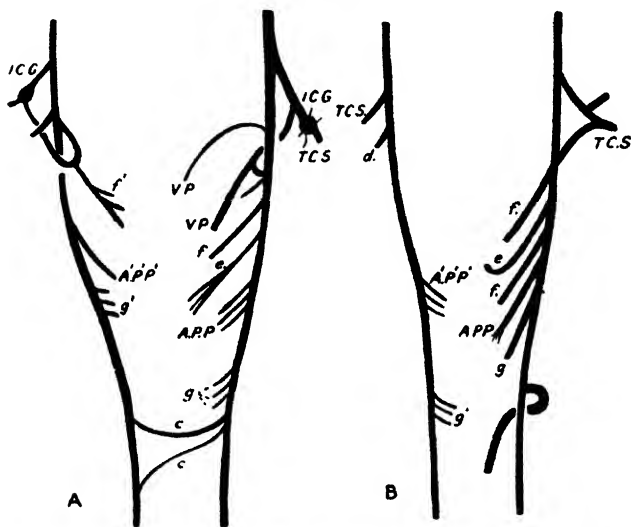
Pulmonary branches may be included within the vagus, or fine filaments may run to the lungs from the upper thoracic ganglia. It may, however, be difficult to trace the latter.

Cardiac Plexus:—The cardiac plexus lies between the aortic arch and trachea, and in some species there is an aggregation of nerves with or without ganglia, lying in the position of the

superficial cardiac plexus. It is connected to the anterior pulmonary plexus on one or both sides, and to a plexus around the main branches of the aortic arch. In some species branches of the vagus and sympathetic reach the cardiac plexus through the latter. The composition of the plexus in the species described in this paper are :—

Felis bengalensis (text-fig. 4):—Two branches from the left vagus (*f*), a twig from the left anterior pulmonary plexus (A.P.P.), and a thick branch from the inferior cervical ganglion of the left sympathetic (C.B.S.). These form a superficial plexus without ganglia. The deep plexus receives a branch from the right vagus (*f'*), a branch from the right anterior pulmonary

Text-figure 11.



Thoracic parts of the vagus nerves in: A. *Mephitis mephitis*; B. *Melurus ureinus*; V.P.: nerve plexus round branches of the aortic arch. Other letters as in text-fig. 4.

plexus (A'.P'.P'), and a branch from the left recurrent laryngeal nerve; but it gets no separate sympathetic filaments.

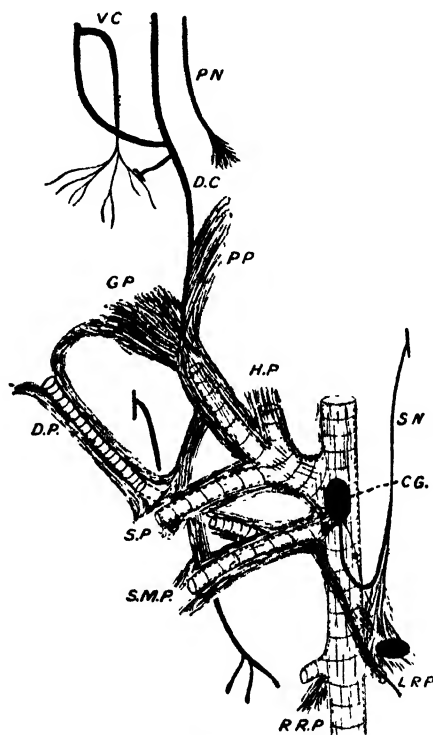
Paradoxurus larvatus (text-fig. 6):—Two offshoots of the left vagus unite to form a cardiac nerve (*f*) which runs to the plexus. No branches of the left sympathetic run directly to the plexus, but they enter the plexus round the branches of the aortic arch (A.V.P.). The right vagus gives two branches (*f*) and the left recurrent laryngeal nerve contributes; but no branches come from the right sympathetic. The plexus communicates with the pulmonary plexus.

Atilax paludinosus (text-fig. 8C):—Each vagus contributes

two branches ($f.f'$) and the left recurrent laryngeal nerve (e) sends a twig. No sympathetic filaments run directly to the plexus on either side.

Genetta felina (text-fig. 7 A):—The left vagus and its recurrent laryngeal branch send each a branch to the plexus, and the former bifurcates (f). The right vagus sends two large cords (f'),

Text-figure 12.



Abdominal parts of the vagus and sympathetic nerves in *Felis bengalensis*

C.G: coeliac ganglia; D.C: dorsal cord of the vagi; D.P: duodenal plexus; G.P: gastric plexus; H.P: hepatic plexus; L.R.P. and R.R.P: left and right renal plexuses; P.N: left phrenic nerve; P.P: phrenic plexus; S.M.P: superior mesenteric plexus; S.N: splanchnic nerve; S.P: splenic plexus; V.C: ventral cord of the vagi.

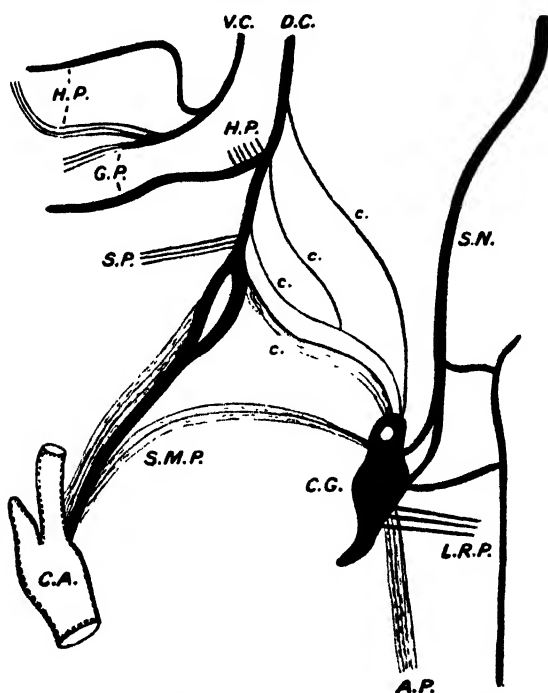
which both divide before reaching the plexus. No separate sympathetic filaments run to it on either side.

In *Civettictis civetta* (text-fig. 7 B) the plexus is formed by a branch from each vagus ($f.f'$) and a brushwork of fibres from the left nerve. Filaments from the left inferior cervical sympathetic

ganglion reach it via the plexus round branches of the aortic arch.

In *Canis thous* (text-fig. 5) the superficial and deep plexuses are very well marked. The former (S.C.P.) receives a thick cord from the left vagus (*f*), several twigs from the right vagus (*f'*), communications from the left anterior pulmonary plexus, and a thick sympathetic filament (C.B.S.). The latter (D.C.P.) is formed by branches of the right vagus (*f'*), left recurrent

Text-figure 13.



Abdominal parts of the vagus nerves in *Paradoxurus larcatus*. A.P: aortic plexus; C.A: cæcum; c: communicating nerves. Other letters as in text-fig. 12.

laryngeal nerve (*e*), and communications with the right anterior pulmonary plexus; but there are no separate sympathetic filaments.

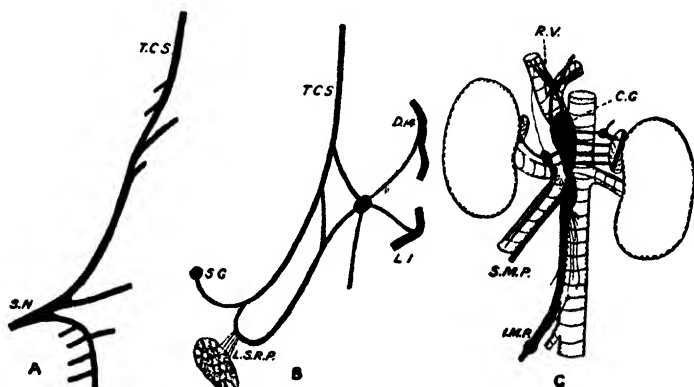
In *Cynictis penicillata* (text-fig. 10B) the cardiac plexus receives a branch from each vagus (*f, f'*), one from the left recurrent nerve (*e*), and communications from the anterior pulmonary plexuses (A.P.P.). No branches come separately from the right sympathetic, but the left inferior cervical ganglion (I.C.G.) sends

numerous fine filaments to the aortic plexus, the latter being connected to the cardiac plexus.

In *Mephitis mephitis* (text-fig. 11 A) a marked plexus grouped round the great vessels (A.V.P.) receives branches from the left vagus and left inferior cervical ganglion. The cardiac plexus receives a twig from each vagus (*f.f'*), one from the left recurrent laryngeal nerve (*e*), and a brushwork of filaments from a right vago-sympathetic loop.

In *Melursus ursinus* (text-fig. 11 B) superficial and deep cardiac plexuses are present and communicate with pulmonary plexuses. The superficial plexus gets a branch from the left vagus (*f*), but both vagi and the left recurrent laryngeal nerve supply the deep one. Neither plexus gets separate sympathetic filaments.

Text-figure 14.



A. *Paradozurus larvatus*, showing the thoracic sympathetic cord (T.C.S.) becoming the splanchnic nerve (S.N.); B. *Canis thous*, showing the thoracic cord (T.C.S.) becoming the great splanchnic nerve, the small splanchnic filaments ending in the left suprarenal plexus (L.S.R.P.) and a sympathetic ganglion giving rami communicantes to spinal nerves (D. 14 and L. 1); C. Solar plexus in *Meles meles*: I.M.P.: inferior mesenteric plexus. Other letters as in text-fig. 12.

The *Thoracic Gangliated Cord* does not always possess the same number of ganglia as intercostal nerves. When ganglia are absent the rami communicantes meet the sympathetic cords in T- or V-shaped junctions. Ganglia may be minute or well-marked but are larger in marine than in terrestrial Carnivora. The splanchnic branches vary as follows:—

a. One thick cord arises on each side in the thorax and breaks up into several filaments before entering the solar plexus:—*Felis bengalensis* (text-fig. 12), *Civettictis civetta*.

b. One large thoracic cord and some fine abdominal nerves constitute the splanchnic nerves:—*Felis domestica*, *Cynictis*

penicillata, *Ictonyx zorrilla*, *Mephitis mephitis*, *Ailurus fulgens*, and *Melurus ursinus*.

c. The thoracic cord becomes the main splanchnic nerve, and the others come from the abdominal sympathetic. The remainder of the sympathetic cord appears as a branch of the main splanchnic in *Paradoxurus larvatus* (text-fig. 14 A). In *Canis thous* (text-fig. 14 B) the main splanchnic cord gives a branch to a ganglion whence the abdominal sympathetic passes caudad, and two long rami communicantes run to the last dorsal and first lumbar nerves.

Branches of the thoracic cord to the aortic plexus vary in prominence.

The *Solar Plexus* varies considerably in details, but it is built on the same general plan in all. It lies on one side of, or is wrapped round the celiac axis. It has always at least one large ganglion, but smaller ones may be present in addition. It receives the dorsal vagus cord and splanchnic nerves, and its offshoots accompany the various abdominal arteries, interlacing at their terminations. Sometimes the hepatic and splenic plexuses are apparently given off from the right vagus. Superior and inferior mesenteric ganglia may be present, and these are most marked in *Meles meles* (text-fig. 14 C). As filaments of the right vagus get into many, if not all, of the offshoots the abdominal organs get a rich supply of both vagus and sympathetic filaments. The following list contains an enumeration of the offshoots:—

- | | |
|--------------------------------|---------------------------------|
| 1. Phrenic plexus. | 7. Renal plexuses. |
| 2. Gastric " | 8. Suprarenal plexuses. |
| 3. Hepatic " | 9. Spermatic " |
| 4. Splenic " | 10. Ovarian " |
| 5. Duodenal " | 11. Inferior mesenteric plexus. |
| 6. Superior mesenteric plexus. | 12. Aortic plexus. |

All the offshoots are not equally obvious in all the Carnivora. The most variable is the duodenal plexus, which depends on the presence or absence of a large duodenal branch of the superior mesenteric artery (text-fig. 12).

The Sympathetic Nervous System in Phocæna communis.

Swan (1), in his description gives the following data:—

1. The pyriform superior cervical ganglion of the sympathetic nerve sends one portion upwards and one downwards.

2. The sympathetic communicates with the superior laryngeal nerve.

3. The inferior cervical ganglion on the right side communicates with the vagus, but the left one does not.

4. The thoracic ganglia are well marked, and on the whole larger than in other mammalia; they give off aortic and

splanchnic nerves, rami communicantes and lateral branches to the *rete mirabile* on the thoracic parietes*.

5. The aortic plexus has a large ganglion.

6. The rectum and bladder receive small nerves.

7. There is no perceptible difference in the nerves to the upper and lower part of the intestines, just as these parts of the gut merge gradually into one another, and there is no capacious cæcum.

It is, therefore, evident that the sympathetic nerves differ in many respects from those in the Fissipede Carnivora.

Swan has also made several generalizations on the sympathetic nerves in the Mammalia, and the conditions described in this paper furnish illustrations of his remarks which, as far as the Carnivora are concerned, were made on a very limited series of animals.

Summary and Conclusions.

1. In most Carnivora Fissipedia the cervical parts of the vagus and sympathetic nerves are fused. In most cases fusion only affects the cords, but in a few species the ganglia are also united. Fusion consists either of an intimate mingling of fibres or adhesion of sheaths only.

2. The ganglion nodosum is frequently absent in both the neck and the foramen lacerum posticum; and the superior cervical ganglion of the sympathetic is likewise absent in a few species.

3. No middle cervical ganglion is present, and inferior cervical ganglia are frequently absent.

4. Sympathetic cardiac nerves are frequently contained entirely in branches of the vagi.

5. The cardiac plexus is sometimes divisible into superficial and deep parts, but ganglia are uncommon.

6. Pulmonary nerves may arise from cardiac branches of the vagi.

7. The plexus gulæ varies in complexity. It may be absent. In most species ventral and dorsal cords produced by a varying degree of intermingling of the vagi pass from thorax to abdomen.

8. The ventral vagus cord supplies the ventral gastric wall and branches run along the lesser curvature to the pylorus.

9. The dorsal vagus cord supplies the dorsum of the stomach. It ends directly in the celiac ganglia or in one of the offshoots of the solar plexus, or it is diffused throughout the plexus.

10. The number of ganglia on the thoracic sympathetic cord does not always correspond to that of the intercostal nerves.

* The *rete* disseminated throughout the body enables the animal to accommodate itself to variations in the water pressure when it dives or rises to the surface; and the sympathetic nerves running to the thoracic *rete* form part of the accommodating neuro-vascular mechanism.

11. The superior and inferior cervical ganglia are variable, but the middle cervical sympathetic ganglia are absent.

12. Thoracic sympathetic ganglia are absent, small or large.

13. The splanchnic nerves may be branches or continuations of the thoracic cords, and a branch of the great splanchnic becomes the abdominal sympathetic in the latter case.

14. Well-marked nerves are traceable from the vagus and solar plexus to the cæcum.

15. The vagus nerve may give off plexuses which arise from the solar plexus in most mammals.

16. The vagus and sympathetic nerves of the terrestrial Carnivora differ in many details from those of *Phocæna communis*, the latter being more complex in several respects.

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3. " " P. Z. S. 1921, pp. 873-876 (Marsupialia).
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5. " " P. Z. S. 1922, pp. 149-156 (*Hyrax*).
6. " " P. Z. S. 1922, pp. 444-449 (*Mandrillus*).



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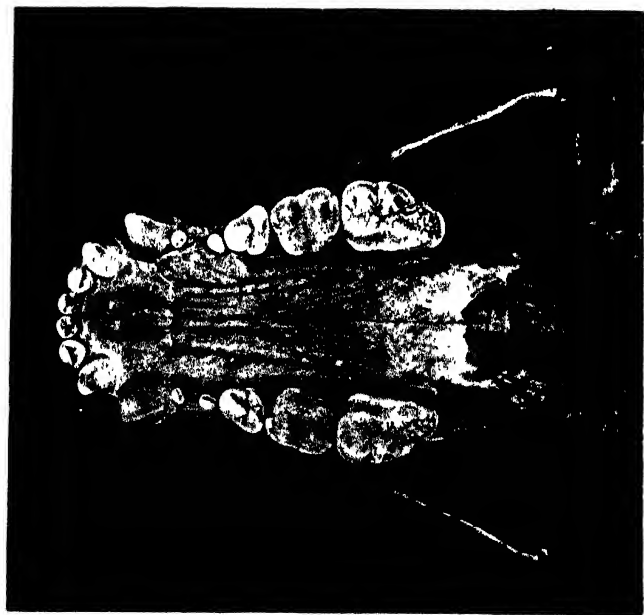


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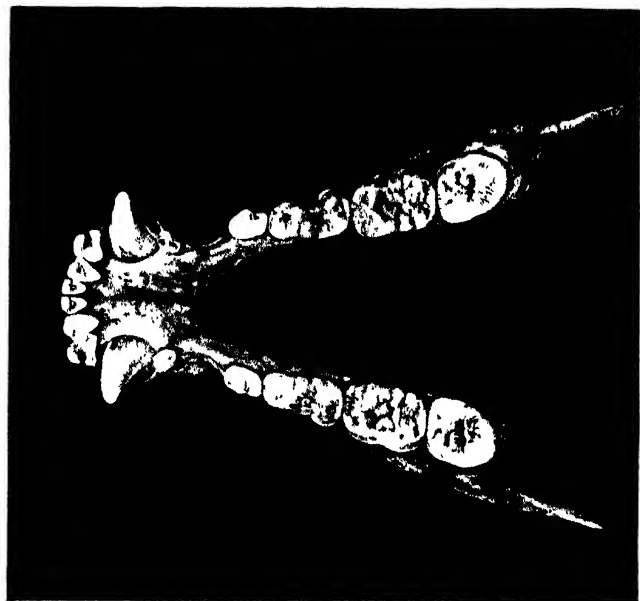


4

PALEARCTIC BEARS.



5



6.

Uppsala, B. & C. 1923

PALEARCTIC BEARS

8. Remarks on some Palearctic Bears.

By EINAR LÖNNBERG, F.M.Z.S., &c.

(Plates I., II.*)

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Among the collections which the Royal Nat. Hist. Museum in Stockholm recently has received from China, chiefly through the courtesy of Professor J. G. Andersson, there is also material of two different kinds of Bears which are likely to arouse great interest. Therefore I take the pleasure of laying before the Society the following notes, in which I endeavour to prove that the *pruinus* Bears must be regarded as so different from other Bears that they should form a separate group of sub-generic value, and also what is to be understood by *Ursus lasiotus* Gray.

A Bear of the pruinus Group.

On the 14th of August, 1921, Mr. D. Sjölander obtained a young Bear, evidently of this group, in the Min-Shan Mountains, South-Western Kansu. With regard to its colour, it does not closely correspond with Lydekker's plate of *U. pruinus* (Proc. Zool. Soc. 1897), but there is an agreement in pattern which may be of more importance. The present specimen has the snout pale yellowish grey, with a dark brown area around and especially below the eye. Forehead and sides of head rather rich buff, but with the concealed parts of the hair blackish brown; on the occiput the colour is rather more cinnamon-rufous. The ears are richly clothed with long, shaggy fur, blackish brown in colour, and the same colour extends also over an area below them. A broad white band extends across the chest and up in front of the shoulders so as to meet dorsally and form a collar around the neck; but a branch also extends backwards across the upper part of the shoulders, so that by this and the collar, a large oval patch of blackish colour (but partly with yellowish tips) on top of the withers (interscapular region) is surrounded, except on the posterior side. From the posterior end of the posterior white branch a rather narrow yellowish-grey stripe continues downwards, and thus helps to define the black fore limb from the body. The back and flanks are black, with more or less numerous yellowish tips to the hairs. The hind limbs are black like the fore limbs. Although the colour differs in the different individuals

* For explanation of the Plates, see p. 86.

(which is a common thing among Bears), the pattern thus described may be recognized on Lydekker's plate, and on Sven Hedin's photos, published by Leche in his report on the zoological specimens collected by that explorer ('Scientific Results of a Journey in Central Asia, 1899-1902,' vol. vi. part 1, Stockholm, 1904). It will appear from this, as well as from the descriptions by various authors, that, in spite of the differences in colour which have been observed on Bears named "*pruinus*" or "*lagomyiarius*," there is a certain pattern common to all. Our knowledge about these Bears is very unsatisfactory, and it is for the present impossible to say whether they constitute more than one species or subspecies; but, nevertheless, they appear to form together a systematic unit, which differs from the common *Ursus arctos* or the genus *Ursus* s. str., to which they usually have been referred. This may be proved by the structure of the feet and the teeth, as will be shown below.

Through the investigations of Mr. R. I. Pocock, it has been proved that the Bears form several natural groups (by him considered as genera), which may be distinguished by means of the different structure of their feet. The disposition of hairiness and nakedness, and the degree in which the digital pads are free from or connected with each other, give the distinguishing characteristics.

An examination of the feet of this *pruinus* Bear gives the following results:—

The digital pads of the second, third, and fourth fingers are basally closely connected, so that there are only shallow depressions between them. The corresponding depression between the fourth and fifth fingers is somewhat broader and more pronounced, while the cleft between the second and first is still deeper. The interspaces between the digital pads are, however, in all cases completely naked. The digital pads of the fifth and, somewhat more narrowly, the first fingers, are connected by a naked area with the plantar (palmar) pad. Between the latter and the digital pads of the second, third, and fourth fingers there is a matting of rather thick and long hairs which are directed forward so as to partly cover the basal parts of the digital pads. This matting appears continuous, but a closer examination proves that it really consists of four patches, because, if the hairs are divided, there is found a hairless tract connecting each digital pad with the plantar pad, although this is concealed by the overlying hairs (*cf.* Pl. I. figs. 1 & 2).

The plantar pad is transverse and somewhat broader on the lateral side. In the present specimen there is only a slight crease visible, opposite the interdigital space between the second and third fingers. It is very widely separated from the carpal pad by a broad and thickly hairy area. The latter pad is rather small, somewhat elongate in shape, but not transversely expanded.

With regard to the relation between the plantar pad and the carpal pad, our *pruinus* Bear thus resembles *Euarctos*, *Ursus*,

and "*Danis*," and differs from "*Arcticonus*" (= *Selenarctos* *), *Tremarctos*, *Helarctos*, &c. The structure of the anterior portion of the fore feet of *pruinus* is, however, very different from that of *Ursus*, because the interspaces between the digital pads are hairy in the latter; in fact, the digital pads of *Ursus* are entirely surrounded by hair, because the naked strips between the digital pads and the plantar pad are so exceedingly narrow that they are even difficult to find when one is looking for them; still less are they plainly visible like those between the digital pads of the first and fifth fingers on one hand and the plantar pad on the other, as is described above, in the case of *pruinus*. With regard to this latter detail, the anterior portion of the fore feet somewhat resembles the corresponding parts of *thibetanus* (as figured by Pocock, 1914), but the digital pads of the latter are much more distinct and free from each other than in the *pruinus*.

The structure of the fore feet of *Euarctos* is essentially similar to that of *Ursus* (at least in a specimen of the Alaska race which I have had for comparison), and it differs thus in the same way from *pruinus*. The fore feet of the Grizzly Bears appear, to judge from Pocock's description, to differ from those of *Ursus* in having the digital pads more connected with each other and without hair between them, in which respect they resemble those of *pruinus*. In Pocock's figure (1918) of the "right fore foot of *Danis horribilis*" there are not to be seen any naked tracts connecting the first and fifth digital pads with the plantar pad, which is so characteristic for the fore feet of the *pruinus*. The latter appears thus to differ from "*Danis*" as well as from the other Bears with regard to the structure of its fore feet.

The digital pads of the hind feet of our *pruinus* are quite fused together basally, although the notch between the first and second toe is deeper than the others. They are not at all separated from each other by hairy tracts. The first and fifth digital pads are broadly connected with the plantar pad by means of a naked area (in the same manner as on the fore feet). Between the three middle toes and the plantar pad is a transverse area thickly covered with hair. If these hairs are divided with the aid of a pair of pincers, there is, however, to be seen a naked strip of skin connecting also these digital pads with the plantar one, although this is not visible without such a proceeding (cf. Pl. I. figs. 3 & 4). The plantar surface is naked to the heel, and there is no notch or depression covered with hair on the hallucal side, only a slight superficial crease indicating the limit between plantar and heel pads. In the absence of this hairy depression on the hallucal side, the hind foot of the *pruinus* differs from *Ursus* and *Euarctos*. Both these genera are also different from *pruinus* in having the

* Sowerby has drawn attention to the fact that Heude already (1901) gave the name *Selenarctos* to an assemblage of Black Bears, among which also *thibetanus* is found; and Sowerby, as "first reviser" of the group, selects this one as the type for Heude's genus (cf. Journ. Mamm. 1930, pp. 216-17).

digital pads surrounded by hair and quite free, not fused basally. The hind foot of "*Danis*" appears more similar to that of *pruinus* by having at least two of the digital pads fused, and the others more closely connected than in the genera just mentioned, and without hair in the interdigital spaces, as well as with regard to the weakness of the hallucal depression and the absence of hairs in the same. The likeness between "*Danis*" and the *pruinus* group is, however, not complete, because judging from Pocock's figure (1918) it has no naked connection between the first and fifth digital pads on one side and the plantar pad on the other. Such a connection is, however, visible in the figure of the hind foot of "*Tremarctos thibetanus*," figured by the same author in 1914; and in fact this figure exhibits several features similar to those of the *pruinus*, but the hind foot of the Thibetan Bear has quite free digital pads and hair in the interdigital interspaces. The fore feet of the latter are also very different in structure when compared with those of the *pruinus* group, as they have a very large carpal pad expanded across the whole plantar surface and only separated by naked and soft skin from the plantar pad.

A comparison between the feet of *Tremarctos* and those of the *pruinus* group is scarcely needed. The fore feet of the former have entirely free digital pads entirely surrounded by hairs, so that a careful examination is needed to reveal the narrow and incomplete connections with the plantar pad. The plantar pad is broadly connected with the rather large carpal pad by means of naked skin on the ulnar side; it extends also backwards on the radial side, and is there connected with a small pad. On the hind feet of *Tremarctos* as well the digital pads are free and rather thickly surrounded by hairs, so that the connections between the digital pads and the plantar pad are entirely concealed until the hairs are artificially divided. With the feet of *Helarctos* those of the *pruinus* group have no resemblance, as the former are much less hairy, and this is, of course, still more the case with those of *Melursus*.

It is thus evident that the structure of the feet of the *pruinus* Bears differs from that of all other Bears, and most certainly from that of *Ursus* s. str. The question is then, whether this difference is also connected with some other morphological differences.

Pocock has demonstrated that the noses of different Bears are different in structure. It is very difficult to judge only from a dry skin, but it appears as if the naked tract between the rhinarium and the upper lip was broader in the present *pruinus* specimen than in, for instance, *U. arctos*, *Euarctos*, *Selenarctos*, and *Tremarctos*, but of course not so broad as in *Helarctos*. In the present specimen, dry as it is, it measures about 1 cm., and is equal in breadth to the nasal septum.

As the *pruinus* Bear from Kansu is rather young, the measurements of its skull have only relative value; but, thanks to the courtesy of Professor N. Holmgren, I have been able to

measure also the skull of a very old male which was brought home from Thibet by Dr. Sven Hedin. The latter skull has the teeth extremely worn, so that their dimensions are of little value, but the other measurements are useful for comparison:—

	Old specimen from Thibet.	Young specimen from Kansu.
	mm.	mm.
Greatest length of skull	351	292
Condylobasal length	331	285
Basicranial length	311	—
Zygomatic width	217	153
Length of nasals	—	90·5
Length of palate from gnathion	189	153
Width of palate inside middle of m^2	51·5	44
Distance from <i>foramen lacrymale</i> to gnathion.	134·5	118·5
Breadth of brain-case	101	101
Interorbital breadth	69	63
Mastoid breadth	157·5	—
Hind margin of m^2 to front of i^1	160	147
Combined length of p^4 , m^1 , and m^2	79	83·2(84)
p^4	18·3×14	18·7×15·5
m^1	24×19	26·5×19·2
m^2	39×21	41×22·2
Combined length of p_4 - m_3	88	95
p_4	—	13·8×8·7
m_1	—	27·5×14
m_2	—	29×18·2
m_3	—	25×18·5

Bear skulls are very variable in shape, and it is thus rather difficult to say whether a certain characteristic exhibited by an individual is of any taxonomic value or not. In the *pruinus* specimen from Kansu the nasals are rather long, and their posterior ends extend much beyond the frontal processes of the maxillary. The mesial length of the nasals is also longer than the mesial frontal suture. In Swedish Bears the opposite as a rule prevails, and I believed, therefore, that this might constitute a characteristic of some importance. This is, however, not the case, because I found later that, in a young Swedish Bear from the province of Jämtland, the nasals were just as in the *pruinus* specimen, being considerably longer than the mesial frontal suture.

For the present it appears very difficult to point out any definite cranial characteristic, which in every case holds good as distinctive between the *pruinus* and *arctos* groups, except those that are derived from the teeth, or stand in connection with their development.

The teeth of the *pruinus* group are, especially the molars, very much larger than the corresponding ones of the *arctos* group (cf. the table above). The same is also the case with p^4 and p_4 . On m^1 of the former the cingulum is quite well marked

off, even on the inner side of the tooth and not only on the outer. On m^2 it is very strongly developed on the inner side, where it forms a distinct shelf (Pl. II. fig. 5). On the outer side it is weaker, but quite traceable. p_4 has a well-developed antero-interior cingulum cusp.

The great size of the molars is relative as well as absolute (cf. Pl. II. figs. 5 & 6). The greatest length of m^2 that I have ever seen when examining a considerable number of Swedish Bears is 35 mm., while the same tooth in the present specimen of the *pruinus* group measures 41 mm. The difference in breadth is still more striking, because m^2 of Swedish Bears is seldom more than about 17 mm. broad, while in the present *pruinus* specimen it even exceeds 22 mm. The combined length of p^4 , m^1 , and m^2 is in Swedish male Bears, as a rule, not more than about 70 mm. and often less, and among the skulls examined by me it was only once 73 mm.; in the young *pruinus*, however, it is as much as 83 (84) mm. The dimension in question is, in adult males of the former kind, less than the distance between m^2 and the *processus postglenoideus*, and also less than the interorbital breadth, but in the *pruinus* the former dimension is larger than the two others.

In *pruinus* the combined length of these three teeth is more than half the mastoid breadth, but in *arctos* considerably less. The superior size of the teeth of *pruinus* may be proved by still more comparative measurements, but the samples mentioned may be enough. It is, however, of interest to observe that the teeth of the *pruinus* specimen are not only absolutely and comparatively larger than those of the typical *arctos*, but also than those of the big Black Bear from Mongolia, which I consider identical with *U. lasiotus* Gray (conf. below), and which belongs to the *arctos* group. This holds good, although this Mongolian Bear is very much larger than *pruinus*; and if the comparison between the combined length of the three teeth mentioned and the other dimensions quoted above is repeated with regard to the Mongolian Bear, the same result is obtained as with *arctos*. By this it appears to be proved that the difference between the *pruinus* and the *arctos* groups is distinct enough in this respect.

The enormous size of the last premolar, and the molars of the lower jaw can also be seen from the table of measurements above, so that further comments on this may not be needed. The big Mongolian Bear is also as regards the teeth of the lower jaw, very much inferior to the *pruinus*.

As the above-recorded measurements prove, the combined length of p_4 , m_1 , m_2 , and m_3 is considerably greater than half the length of the palate in the adult *pruinus**; but in the Bears of the *arctos* group—the big Mongolian one (cf. below) included—the former measurement is even less than half the length of the palate in the adult males. In the latter the combined length of the

* The much worn teeth of the very old specimen do not give very satisfactory measurements, but the corresponding dimension of the young animal must be compared with the palatal length of the older one.

teeth mentioned is about equal to half the mastoid breadth, or perhaps hardly that, but in the *pruinus* group the former measurement is about from 56 to 60 per cent. of the latter.

In consequence of the great size of the mandibular teeth and the resulting great length of the tooth series in *pruinus*, m_3 has been pushed backward, so to speak, so that the posterior portion of the same is concealed by the *processus coronoideus* when viewed from the side. This characteristic, which also has been observed and mentioned by Leche when he described the mammals brought home from Thibet by Dr. Sven Hedin (*l. c.*), serves easily to recognize a mandible of the *pruinus* group, because in the now living Bears of the *arctos* group, m_3 is in its whole extent visible in front of the *processus coronoideus*.

Of the Grizzly Bears, I have unfortunately no material for comparison, but with regard to the skull of a fossil Cave Bear I have had the opportunity of stating that it exhibits the same relative dimensions as the recent *arctos* in the cases mentioned above. Thus the combined length of p^4 , m^1 , and m^2 is shorter than the distance between m^2 and the *processus postglenoideus*, and likewise the former dimension is shorter than the preorbital width and less than half the mastoid breadth. The combined length of p_4 , m_1 , m_2 , and m_3 of the same skull is even contained $4\frac{1}{2}$ times in the length of the palate, and is less than half the mastoid breadth.

In consequence of these facts, I am inclined to consider that the Bears of the *pruinus* group (whether it consists of only one or more species or subspecies) are so different from other Bears that they are entitled to subgeneric rank. This new subgenus I propose to call *Mylarctos*: it is characterized by its very large molariform teeth and foot structure, as described above.

URSUS LASIOTUS Gray.

A fine, big male Bear, procured in Northern Mongolia by the Swedish missionary, Mr. Larsson, and through the courtesy of Professor J. G. Andersson presented to the Stockholm Museum, must, according to my opinion, be named as above. It agrees with Gray's short description, being black with brown nose and somewhat brownish on the head in front of the ears, in consequence of such tips to the hairs. The ears agree with the specific name, being richly covered with long black hairs as well inside as outside. On the sides of the neck there is in some shades of light a faint chestnut-reddish lustre. The under-fur is well developed and dark brown. The claws blackish horn-coloured. In a mounted state the specimen stands a little more than 1 m. at the fore quarters.

Gray's name (*lasiotus*) of 1867 has by later authors been more or less discarded. Even in 1869 Selater identified Gray's Bear with *U. piscator* Pucheran, which latter name referred to a Bear from Kamtschatka. It is true that not much is known concerning Gray's *lasiotus*. It was "imported from Northern

China, and was stated to come from the interior of that country" (Sclater). There appears, however, to be little reason to believe that an animal with such a history came from Kamtschatka. On the contrary, it must be considered far more probable that it really has come from the northern or interior parts of the Chinese empire, *e. g.* from Mongolia. As it is now proved that in fact a Bear with an exterior appearance agreeing with Gray's description of *U. lasiotus* lives there, I am inclined to identify it with Gray's Bear.

It is therefore a matter of secondary importance to make out whether this big Black Bear of Mongolia and the interior of China is identical or not with the Fishing Bear of Kamtschatka. As long, however, as nothing is known about this, all kinds of guessings are unnecessary, and Gray's name *U. lasiotus* may stand for the big and Black Mongolian Bear*.

Dimensions of the skull of the Mongolian Black Bear,
Ursus lasiotus Gray.

	mm.
Greatest length	387
" width	218
Interorbital width	80
Depth of muzzle at front end of nasals	65
" " just in front of orbits	83
Width of muzzle across alveoles of canines	78
" palate inside m^1	48.3
" " posterior part of m^2	47
Least width of palate behind molars	44
Width of palate at the premolar diastema	60
" skull outside middle of m^1	82.5
" brain-case	100
Length of nasals mesially	117
Greatest combined breadth of nasals	37
Distance from hind margin of palate to gnathion	188
" " orbit to gnathion	147
Front of canine to back of m^2	132
Combined length of p^4 , m^1 , and m^2	75
Length of p^4	10.5
Breadth of p^4	13.3
Length of m^1	24
Breadth of m^1	17
Length of m^2	35.3
Breadth of m^2	18.5
Length of lower jaw	253
Depth of lower jaw at middle of m_3	59
Combined length of p_4 , m_1 , m_2 , and m_3	84.5
m_1	24.3 × 12.3
m_2	24.8 × 16
m_3	22.2 × 15.

* Since writing the above I have had the opportunity of seeing some Bears from the Kamtschatka Peninsula which I suppose must be regarded as *Ursus piscator* Pucheran. There has been no time for a thorough examination of the skulls, but the skins certainly look very different from the specimen which I consider to be

Mr. A. Sowerby has recently published a review of "Heude's Bears in the Sikawei Museum and on Bears of Palearctic Eastern Asia." In this paper he accepts Heude's specific name *cavifrons*, and attaches the same to a Bear of N.W. Manchuria. Sowerby himself has shot a Bear of this kind in N. Kirin, Manchuria. According to the description, the exterior of this Bear must be very similar to that of the present specimen, as it is said to be "generally black, merging into brown on the muzzle; brownish on the head:" So far there is nothing which prohibits the specific identity of this Bear with Gray's *U. lasiotus* and the present specimen.

Mr. Sowerby has also published some measurements of his Bear from Kirin, which may be compared with the corresponding ones of the present specimen as recorded in the accompanying table. The greatest length of the skull of Sowerby's Bear is recorded as 16 in., or about 405 mm., thus only 18 mm. more than the present specimen. The greatest width of the former is 9.25 in. or about 234 mm.; the interorbital width is about 88 mm. If "greatest width of cranium" is to be understood as width of brain-case, this dimension, about 108 mm., is rather similar to that of the present specimen. Some of the other measurements recorded by Sowerby are less easily understood, and some are certainly larger than those of the present specimen. This is especially the case with the length of the lower jaw. As the Bears generally are very variable, it is difficult to decide whether these two are to be regarded as belonging to the same species or not, for the negative conclusion emphasizes the fact that Sowerby refers Heude's *cavifrons* to "*Spelæus*." As characteristic of the latter he mentions "very high foreheads so that the cranial outline at this point is strongly concave." Heude's figure of the type shows also such a condition. In opposition to this our Mongolian Bear shows a cranial outline which at the forehead is nearly straight. The question then presents itself: How much value can be attributed to such a characteristic as a more or less concave or straight facial profile line? With my knowledge about our Brown Bears in Sweden, I am not inclined to overrate this characteristic, because I have found that it is very variable in them. We have, for instance, from the same tract of Southern Lapland, Bear skulls with straight profile and others with the profile just as concave as Heude's figure of *cavifrons*. This fact does not, of course, prove that the variability of the Bears of Mongolia and Manchuria in this respect is as great as in Europe, but there is always the possibility or even probability that this is the case.

The important cranial characteristic which Gray mentions as

U. lasiotus Gray. They are all much paler than the latter—brown, brownish grey or lighter,—but even if they had been black, and I am told there are also very dark or black Bears in Kamtschatka, I think that such specimens must be easily recognized by their softer and much more shaggy fur than the Mongolian Bear. Bears which I have seen on several occasions in Zoological Gardens under the name of *U. piscator* were also similar to the present Kamtschatka skins.

distinguishing the Grizzly Bears from the true *Ursus* of the *arctos* group, viz. "the palate narrow and contracted behind," is not mentioned for "*cavifrons*," and it is not known if its palate has this characteristic shape or not. If such should happen to be the case, our Mongolian Bear has nothing to do with it, because the latter has a broad palate, which is not more contracted behind the molars than is the case with true *arctos*; and it therefore certainly belongs to the same group as the latter.

Mr. Sowerby also mentions another of Heude's Bears, called by the latter "*Ursus mandchuricus*." It is also a large and dark Bear, although not so black as "*cavifrons*," and is said to have a "fairly straight cranial outline." It is possible that this is identical with Gray's *lasiotus*, and, if such is the case, the latter name of course has priority. The question about the identity can hardly be decided for the present, but so much ought to be certain, that nothing prevents Gray's name from being laid on the present big and Black Bear from Mongolia, which evidently is a member of the *arctos* group.

With regard to the general size, the Mongolian Bear appears to be larger than the European, and the greatest length of the skull of the former (387 mm.) is larger than that of any Swedish Bear skull I have seen. The three largest specimens of the latter kind that I have had the opportunity of measuring, have had maximum lengths of 362, 367, and 372 mm. With regard to the zygomatic width, the Mongolian Bear is not superior to some of the largest Swedish Bears. On one occasion I found the same breadth, viz. 218 mm., in one of the latter, but several times still greater dimensions, e. g. 223, 225, 229, and even 231 mm. The latter is thus similar to Sowerby's specimen in breadth. With regard to the interorbital width (80 mm. in the Mongolian Bear), I have seen several Swedish Bear skulls as large or still broader, e. g. 80, 83 (twice), 84, and 89 mm.—the last thus fully equal to Sowerby's specimen. Otherwise the Mongolian Bear is greater in most dimensions or near the maximum. The palate is, however, often broader in male Swedish Bears.

The comparative size of the teeth is to be seen from the following:—

p^4	in the Mongolian specimen	16.5 mm.;	in Swedish male Bears	15-16.5 (once 17.5 and once 18) mm.
m^1	"	"	24 mm.	" " " 21-23 (once 20) mm.
m^2	"	"	35.3 mm.	" " " 32-35 (once resp. 81, 30, and 29 mm.).

The difference in this respect is therefore not so very great. Unfortunately, Sowerby has not given any measurements of the teeth of "*cavifrons*," but Heude's figures of the teeth, which are said to represent the actual size, do not indicate that the teeth of his Bear are larger than those of an average Swedish Bear, and m^2 appears to be rather narrow.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. Photograph of the lower side of the right fore foot of a *pruinus* Bear (skin) from Kansu.
,, 2. Diagram of the lower side of the right fore foot of a *pruinus* Bear to show the distribution of the hairy areas and the connections between the digital pads and the plantar pad.
,, 3. Photograph of the lower side of the right hind foot of a *pruinus* Bear (skin) from Kansu.
,, 4. Diagram of the lower side of the right hind foot of a *pruinus* Bear to show the connection between the digital pads and the plantar pad.

PLATE II.

- Fig. 5. Upper jaw with dentition of a young *pruinus* Bear from Kansu.
,, 6. Lower jaw with dentition of a young *pruinus* Bear from Kansu.

9. Some Notes on *Leander longirostris* M. Edwards, and other British Prawns. By ROBERT GURNEY, M.A., F.L.S., F.Z.S.

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(Text-figures 1-6.)

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The European Prawns of the genus *Leander* have been very thoroughly revised by De Man*, who has shown that *L. longirostris* occurs commonly on the Dutch coasts, where it has hitherto been recorded under the name of *L. squilla*. The two species closely resemble one another in respect of the form of the rostrum, but differ greatly in other respects, and De Man's very careful and detailed description has made discrimination of the species an easy matter.

In Norfolk a prawn has long been known to occur in the lower reaches of the rivers flowing into Breydon Water, and has been recorded by Mr. A. H. Patterson† and myself‡ under the name of *L. squilla*. Having obtained a number of specimens of this prawn from Breydon Water in June 1921, a careful examination of these specimens was made, with the result that it became perfectly clear that they could not be referred to any species hitherto recorded as British. Subsequent reference to De Man's paper at once proved them to belong to *Leander longirostris* M. Edw. An examination of old material and of specimens since collected in the Norfolk rivers and at various points on the coast has shown that *L. squilla* does not normally occur at all in any part of the rivers, but that it is quite common between tide-marks on the coast.

I have also visited the estuaries of the East Coast from Norfolk to the Thames, and have not been able to obtain any evidence of the occurrence of *L. longirostris* anywhere except in Breydon Water and the rivers entering it.

* De Man, Tijdschr. Nederl. Dierk. Vereen. (2) xiv. p. 115 (1915-16).

† Zoologist, (4) ii. p. 178 (1898).

‡ Trans. Norfolk & Norwich Nat. Soc. vii. p. 637 (1904).

It may be of interest not only to give some account of the distribution and habits of *L. longirostris* in Norfolk, but also to add some notes on the remaining four species of British Prawns.

The structural specific differences have been dealt with so thoroughly by De Man that it is not necessary to repeat them in great detail, but I have added some account of the colour of living specimens, since the species may readily be distinguished when alive by colour alone, and this is a character to which sufficient importance has not been attached. Some account is also given of the range of variation of certain characters which are regarded as of specific importance.

In the following table, measurements are given of typical examples of the five British species. For purposes of comparison the absolute measurements of the antennule and second leg have been converted into percentages of the peduncle and dactylus respectively. There is much individual variation, and the proportions of these parts are very different in immature specimens, so that such selected examples can only be taken as a general guide; but they illustrate very well the characters of the differences generally to be observed.

TABLE I.

Measurements of typical individuals of the British species of Prawn. The measurements for 2nd leg and antennule are converted to percentages of the dactylus and peduncle respectively.

	Locality.	Total length.	Rostrum.	2ND LEG.					1ST ANTENNA.			
				Dactylus.	Chela.	Palm.	Carpus.	Merus.	Peduncle.	Shorter outer flagellum.	Basal part.	Accessory part.
<i>L. serratus</i> ♂ ...	Burnham.	88 mm.	7 4	100	191	91	100	133	100	83	16	66
<i>L. squilla</i> ♀ ...	Thornham.	57 "	8 3	100	303	203	290	258	100	106	47	57
<i>L. adspersus</i> ...	Poole.	68 "	6 3	100	229	129	195	183	100	122	39	83
<i>L. longirostris</i> ..	Breydon.	69 "	8 4	100	266	166	246	233	100	65	17	48
<i>P. varians</i>	Cley.	43 "	5 2	100	300	200	410	235	100	80	58	21
"	"	38 "	6 2	100	253	153	286	244	100	107	77	30

Key for determination of the Species.

- | | |
|--|-----------------------------|
| 1. Carpus of 2nd leg much shorter than merus | <i>L. serratus.</i> |
| Carpus longer than merus | 2. |
| 2. Carpus of 2nd leg longer than chela | <i>Palæmonetes varians.</i> |
| Carpus shorter than chela | 3. |
| 3. Dactylus of 2nd leg one-third the length of the chela | <i>L. squilla.</i> |
| Dactylus nearly or quite one-half length of chela | 4. |
| 4. Short flagellum of antennule as long as or longer than peduncle | <i>L. adspersus.</i> |
| This flagellum much shorter than peduncle | <i>L. longirostris.</i> |

1. LEANDER SERRATUS (Pennant).

Colour.—Thorax and abdomen strikingly banded with brownish red, the lines on the thorax running almost horizontally, or obliquely forwards and upwards. Rostrum covered with small red chromatophores. Legs banded with purple and yellow.

Rostrum slender and greatly exceeding the length of the antennal scales. It is conspicuously upturned and devoid of spines in its distal third. The apex is bifid, and the usual number of spines is 7 dorsally and 5 on the ventral margin. The first spine is situated well behind the eye, and the second either above or slightly behind it.

De Man (*ibid.* p. 169) has described three specimens in which the rostrum was of abnormal form, and I have had the opportunity of examining two specimens in the museum of the Marine Laboratory at Plymouth which are of some interest. In both these cases (measuring 57 and 54 mm.) the rostrum is straight, without the upturned toothless portion characteristic of *L. serratus*, the apex undivided. The spine-formula is $\frac{6}{2}$ and $\frac{7}{2}$.

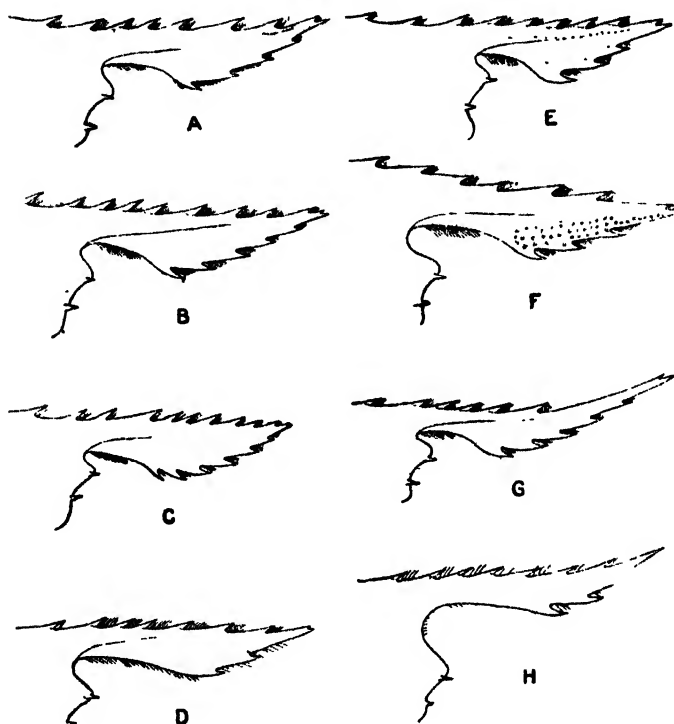
In both cases the general resemblance of the rostrum to that of *L. squilla* was rather striking, and they also agreed more with *L. squilla* in having the short flagellum of the antennule approximately equal in length to the peduncle. On the other hand, the form of the second leg, and in one case the palp of the mandible (that of the other was not seen), left no doubt that these were two abnormal examples of *L. serratus*.

In quite young specimens up to about 25 mm. the rostrum alone is by no means a safe guide to identity. In the autumn on the South Coast young *L. squilla* and *L. serratus* are found commonly in rock-pools mingled together, and their separation is not altogether easy. In such specimens the length of the dactylus of the second leg is also an unreliable character, since this joint in specimens of *L. squilla* up to 15 mm. may nearly equal the length of the palm, and the adult form is only gradually assumed. On the other hand, the antennule provides, as I believe, a safe means of separating the two species. In such small specimens of *L. squilla* the free part of the shorter ramus is much shorter than

the fused* part, whereas in *L. serratus* it is considerably longer.

Antennule.—The short flagellum is about one-seventh shorter than the peduncle, and the fused part one-quarter or one-fifth of its total length.

Text-figure 1.



Rostrum.

- A. *Leander longirostris*. B, C. *L. longirostris* with unusual number of teeth. D. *Palæmonetes varians*. E. *L. squilla*. F. *L. adspersus*. G. *L. serratus* (adult). H. *L. serratus* (young, 15 mm. long).

Second Leg.—Dactylus nearly half the length of the chela; carpus shorter than the chela or the merus.

Distribution.—This, the so-called "Common" Prawn, is a littoral species, preferring, but not confined to, weedy and rocky ground. It is abundant on the south coast of England and on

* The inner, shorter, branch of the outer flagellum is usually described as being fused to the outer branch for part of its length, and the terms "fused" and "free" part are convenient and intelligible. But the "free" part is clearly shown in development to be a secondary or accessory outgrowth of the basal, sensory, part of the flagellum. The basal part, plus the accessory flagellum, is here spoken of as the "shorter flagellum" simply for convenience of description.

some parts of the Irish coast, but it is by no means common on the East Coast north of the Thames. Murie* has given an excellent account of the distribution of this prawn, to which I can add little. The shrimpers from Southend and from Burnham-on-Crouch bring in fair numbers of them, but at West Mersea they are much more rare. I have been to sea with one of these shrimpers and saw only one prawn in a catch of 12 gallons of "Pink Shrimps" (*Pandalus montagui*). At Harwich also the prawns brought in are so few as to be hardly worth the trouble of separating them from the shrimps. They are said to be taken at times in some numbers in the Orwell and Deben, and I have myself taken them as far up the Deben as Woodbridge. At Aldeburgh the species is so rare that a fisherman who took one among his shrimps in 1921 had never seen one before! Off Yarmouth the capture of prawns is exceptional, though a few are sometimes taken on the sandy ground close inshore, and I have myself seen specimens taken on Breydon Water. At Lynn it appears to be almost unknown.

L. serratus has been recorded from Oresund (Denmark), and is found on the coasts of Holland, Belgium, France, and the Channel Islands. In the Mediterranean it occurs in "prodigious quantities" on the coast of Algeria (Lucas), and inhabits the shores of Italy, Greece, and the Bosphorus.

It is therefore a southern species, which is only a straggler in the North Sea.

Breeding-period.

Whereas the other species of British prawns breed during a well-defined period in summer, the breeding-period of *L. serratus* seems to extend through winter and to continue till midsummer. In the List of the Plymouth Marine Invertebrate Fauna† it is recorded as breeding from November to June, but egg-bearing females may still be found in July. I have little personal acquaintance with this species, since it is so rare off the Norfolk coast, but it seems to me that the few published records indicate that *L. serratus* may prove to have a breeding-habit somewhat similar to that of *Crangon vulgaris*. In this species Ehrenbaum‡ found two main periods of egg-laying—namely, April–June and October–November. The autumn-laid eggs took 4 to 5 months to develop, and hatched from February to April, while those laid in summer hatched in about 4 weeks—i. e., from May to August.

Larvæ of *L. serratus* are found in very small numbers in the plankton from December onwards.

Owing to the difference in the breeding period, any *Leander* larvæ found off British coasts from December to nearly the end of June may confidently be assigned to *L. serratus*.

* Report on the Sea Fisheries and Fishing Industries of the Thames Estuary, p. 247. London, 1903.

† Journ. M. B. A. vii. (1904).

‡ Mitth. der Sekt. für Küsten und Hochseefischerei, Jg. 1890.

2. LEANDER SQUILLA (Linn.).

Colour.—Both thorax and abdominal segments bear dark yellow-brown bands, which are usually very conspicuous, and are retained for a long time even in specimens preserved in formol, though rapidly disappearing in spirit. The rostrum is sometimes quite colourless, but generally small red chromatophores are scattered over it or arranged in a median row. Kemp states that the rostrum is without chromatophores, but this is exceptional in my experience of Norfolk specimens. The eye-stalks and peduncles of the antennules are deeply pigmented with purple-brown, and the same is the case with the basipodite and ischium of the third, and sometimes of other, legs. The joints of the legs are marked by bands of yellow pigment, and the palm of the chela of the second legs is bright blue. The intensity of the colour seems to vary to some extent with locality and season. In the summer of 1921 all the prawns, of all ages, taken in Wells Harbour, were brilliantly coloured as described above, the blue of the chelæ being particularly conspicuous. But others taken from rock-pools at Whitsand Bay in the spring of 1922, though showing the same distribution of colour, were by no means conspicuously banded. They could, however, be immediately distinguished from *L. serratus* of the same size by their darker colour. Again, the colouring of the prawns in Wells Harbour during the summer of 1922 was far from being so pronounced as in the previous year, and many, particularly the males, were found to be almost colourless. The blue colour which was so striking a feature of the chelæ in 1921 was seldom brilliant, and often absent, in 1922.

Length. Male 28–50 mm. Female 30–63 mm.

The great range in size is due to the fact that maturity is reached in the first year at an average size of about 40 mm. for females and 30 mm. for males. Females over 50 mm. may be assumed to be two years old, and it is probable that those of 60 mm. and more are in their third year.

Rostrum broad, very slightly upcurved, armed dorsally with 7–9 teeth, two of which are placed behind the eye, and the third above or slightly behind it. A minute apical tooth is almost invariably present in addition. Ventral teeth usually three. The number of these teeth varies within very narrow limits. For 114 females from Wells, in Norfolk, the number of teeth was as follows:—

Dorsal teeth:	9	8	7	6
No. of individuals:	12	65	36	1
	10.5%	57%	31.5%	.86%
Ventral teeth:	4	3	2	
No. of individuals:	1	112	1	
	.86%	98.2%	.86%	

Adding 62 specimens from various localities on the East Coast south of Norfolk the frequency is somewhat changed :—

Dorsal teeth :	9	8	7	6
Individuals :	22	101	52	1
	12.5%	57.4%	29.5%	57%

There seems to be a somewhat higher frequency for 9 dorsal teeth than there is in Norfolk, but the number examined is not sufficient for a definite conclusion. De Man's figures for 106 specimens from various localities are as follows :—

Dorsal teeth :	9	8	7
Individuals :	20%	66%	13%

In the typical form of *L. squilla* from Scandinavia, De Man found seven dorsal teeth in 31 per cent. of specimens and nine teeth in 18 per cent.

Such figures as these seem to indicate a definite local variation in respect of this character, but in my opinion the material examined is only sufficient to indicate a probability that such variation occurs.

Mandible palp.—*L. squilla* differs from all other European species of *Leander* in having the mandible palp two-jointed. This difference was first pointed out by Dr. W. T. Calman*, but the palp was correctly figured by Ortmann in 1901†, though not alluded to in his definition of the genus *Leander*. This character cannot be used in the determination of young specimens 20 mm. or less, since, in *L. longirostris* at all events, the mandible palp is still often two-jointed at that size.

Antennule.—The short flagellum is approximately equal in length to the peduncle, but may be either shorter or longer than it. This flagellum exceeds the length of the peduncle more frequently in the male than in the female. The free part generally exceeds the fused part in the proportion of 5 to 4.

Second Leg.—The second leg reaches, when extended, beyond the antennal scale by the whole chela or even by part of the carpus as well. The dactylus is conspicuously shorter than in the other species, being usually about one-third the length of the whole chela. The carpus nearly always slightly exceeds the length of the merus.

De Man, as the result of the examination of large numbers of

* See Kemp, "The Decapoda Natantia of the coasts of Ireland." Fisheries, Ireland, Sci. Invest. i. 1908, p. 127 (1910).

† "Die Klassen und Ordnungen der Arthropoden." Abth. Crustacea Malacostraca, Taf. lxxiv. fig. 2 e (1901).

L. squilla from many localities, has come to the conclusion that three varieties or geographical races should be separated :—

- (1) *L. squilla*, typical form.
Scandinavia and the Baltic Sea.
- (2) *L. squilla* var. *intermedia* De Man.
Holland, British, and probably French coasts.
- (3) *L. squilla* var. *elegans* Rathke.
Mediterranean, Black Sea, Azores, Madeira, Canaries,
Cape Verde Islands.

These varieties are separated by very slight differences, the most important and constant of which relate to the antennule—thus :—

- (1) Fused part of short flagellum a little shorter or a little longer than the free part, rarely equal to it.
Typical form.
- (2) Fused part distinctly shorter than free part.
var. *intermedia*.
- (3) Fused part distinctly longer than free part.
var. *elegans*.

Norfolk specimens agree with the description of the variety *intermedia*, but it is possible, as De Man suggests, that *L. squilla* from Scotland may prove to belong to the typical northern race. I have not had the opportunity of examining specimens from the east coast of Scotland, but a male received from Millport on the west undoubtedly belonged to the var. *intermedia*, since the free part of the flagellum exceeded the fused part in the proportion of 5 : 4.

Distribution in Britain.—*L. squilla* appears to be distributed all round the coasts of England, Ireland, and Scotland, even as far as the Shetlands. It is a littoral species living between tide-marks, and I have found it to be abundant all along the Norfolk coast from Hunstanton to Cley. At Wells it can be caught in quantities by working a hand-net along the wooden quay-heading at high tide. The pools on the salt marshes at Wells are tenanted for the most part by *Palæmonetes varians*, but some were found in August to contain *L. squilla* in addition. At Thornham numbers were taken on the woodwork of a sluice, and I have found that such sluices, where a pool of water remains even at low tide, are favourite resorts for this species. In such situations it is quite commonly associated with *P. varians*, and it runs far up the East Coast estuaries, but it appears to be none the less intolerant of fresh water, and to abandon a sluice when a large quantity of fresh water is being discharged. It does not normally occur on Breydon or in any part of the rivers Yare, Bure, or Waveney. A single small specimen was, however, taken in

1921 by Mr. O. Hunt at Acle at a time of exceptionally high tides. I have taken it myself at the following places:—

R. Crouch at Burnham and Battlebridge.

Blackwater at Maldon.

Mersea Island.

R. Stour at Harwich and Wrabness.

R. Deben at Woodbridge.

I was unable to find it in the Alde between Aldeburgh and Iken, or in the Orwell at Pinmill.

Breeding-period.

In Norfolk the first eggs are laid about the end of May or beginning of June. One female, taken on June 1 with eggs apparently very recently laid, hatched her young on July 5, the eggs having therefore been borne 35–40 days. This result is in general agreement with Mr. Elmhirst's figures*. Mr. Elmhirst kept observation on *L. squilla* in rock-pools at Millport, and found the period of development to depend on temperature as follows:—

	Period of development.	Average temperature.
1921	30 days	23° C.
1911	40 days	14.5° C.
1912	56 days	11° C.

Development may therefore be taken as requiring about 6 weeks under usual conditions.

Breeding continues actively through June and July. In 1921 it ceased about the middle of August, but in 1922 it was continued into the first week of September—a period of about 100 days. Each breeding female seems to produce two broods in the season. In July females with eggs in an advanced stage of development always have the ovary distended with eggs of the second brood, while in August the ovary is usually empty. The production of two broods in the year was established by Mortensen† for *L. adspersus* and by Ehrenbaum for *Crangon vulgaris*, but Mortensen found that it only applied to the larger prawns. In Norfolk, on the other hand, not only does practically every female breed down to a size of about 30 mm., but the majority, at all events, produce second broods. In July the population of females may be separated into two groups—namely, a small number of large prawns from 63 mm. to about 48 mm., and the remainder of smaller prawns among which sizes of 36–39 mm. are the most frequent. These two groups no doubt comprise prawns of two years' and one year's growth. The former on July 25 for the most part bore eggs in early stages having hatched their first brood, while a large proportion of the

* Scottish Mar. Biol. Assoc. Ann. Rep. 1921, p. 7.

† Vid. Undersøg. paa Fiskeriernes omraade udgivne af Dansk Fiskeriforening, i. (1897).

one-year group carried eggs approaching hatching or showed signs of having recently hatched young. It is probable, therefore, that the older prawns spawn before the younger ones.

The period of larval development has been ascertained by Mortensen to be about 4 weeks in *L. adspersus*, and is probably much the same for *L. squilla*. I have not been able to keep the larvæ through more than one moult, so have no direct evidence to offer. No post-larval prawns are to be found at Wells in July, but about the middle of August they begin to appear, and become abundant both in the marsh-pools and in the fucus growing on the woodwork of the quay. In 1922, young did not become abundant till the middle of September, but some then measured 22 mm. and must have been in the harbour for some time. For the most part the smallest young taken measure about 12 mm. Since the young in the first and second post-larval stages do not exceed 9 mm., it seems that metamorphosis occurs out at sea, and that the young do not usually reach the shore till after three or four moults. A very small proportion of the young prawns found in September 1922 were either in the first or second post-larval stages, and these must certainly have been brought in by the flood-tide and have metamorphosed on the spot. On the other hand, in spite of much search, I have only taken one larva in Wells Harbour, and there can be no doubt that the whole larval life is normally spent out at sea. This is in agreement with Mortensen's conclusions with regard to *L. adspersus*.

The proportion of adult males to females was only noted accurately on two occasions—in Wells Harbour on July 25, 1922, and in Blakeney Harbour on August 10. In the former case 37 males were found among 114 females, while in the latter the males exceeded the females, the numbers being 69 males and 56 females.

3. LEANDER ADSPERSUS Rathke.

Palæmon rectirostris Zaddach, 1844.

Palæmon leachii Bell, 1853, p. 307.

Leander adspersus var. *fabricii* De Man, 1916.

Colour.—Unlike the other British species of *Leander*, *L. adspersus* has no bands of colour on either thorax or abdomen, but the body appears of a uniform yellowish grey, due to small black or reddish-black chromatophores scattered irregularly. The rostrum is covered with chromatophores, which are concentrated on the lower half in the form of red or sometimes purplish-red blotches, which, as Kemp has pointed out, provides a conspicuous feature by which the species may be recognized at a glance. The long flagella and the peduncle of the antennule are also very red and the legs banded with yellow, but without the blue on the chela, which is so striking in *L. squilla*.

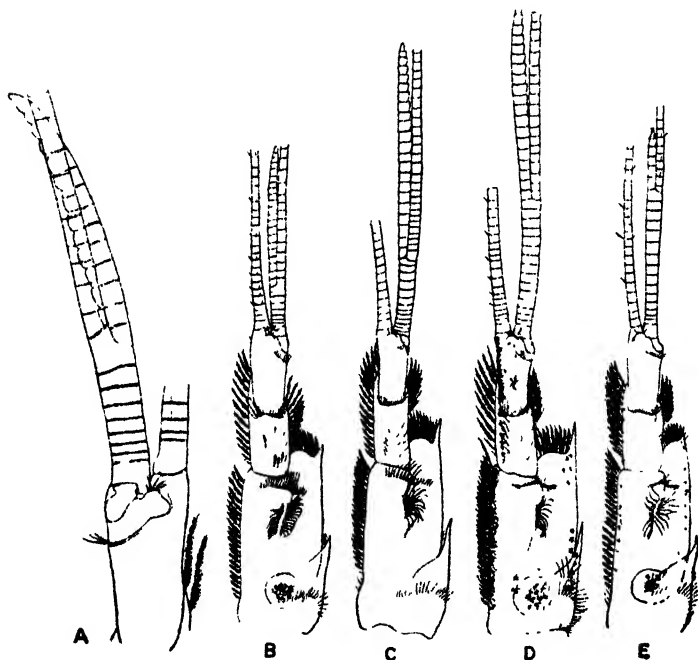
Rostrum.—The rostrum usually extends well beyond the antennal scales, is nearly straight, not very deep, and provided as a rule with 6 spines above and 3 below in addition to the small terminal spine. Only one of the dorsal spines is situated behind

the eye, the second usually slightly in front of the orbital notch. The dorsal teeth differ slightly from those of *L. longirostris* and *L. squilla* in being more depressed.

Mandible palp.—Three-jointed, the second joint about one-third the length of the last joint.

Antennule.—The shorter ramus exceeds the length of the peduncle, and is "fused" to the longer flagellum by only about one-third of its length. The length of the free part is a very noticeable character of the species. There are certain minor

Text-figure 2.



Antennule of female.

A. *L. longirostris*, drawn from moulted skin.

B. *L. longirostris*. C. *L. adspersus*. D. *L. squilla*. E. *P. varians*.

differences in the structure of the peduncle between the species of *Leander* and *Palaemonetes*. These relate to the proportional length of the joints and the form of the stylocerite and terminal plate, but they are less easily described than illustrated. In text-fig. 2 the antennules of the different species are drawn side by side to such scales that the peduncle is represented as of the same length in each case. The proportions of the joints and of the flagella are in this way made clear.

Second leg.—Extends beyond the antennal scales by the

dactylus and part of the palm. The dactylus is long and slender, more than three-quarters of the length of the palm. The carpus usually considerably exceeds the length of the merus, but may be of the same length.

De Man has separated this species into two forms:—

L. adpersus (Rathke). Black Sea.

L. adpersus var. *fabricii* (Rathke). Scandinavia, Baltic, Denmark, France, Adriatic, Mediterranean, British Isles.

The chief differences are as follows:—

Rostrum usually with 4 ventral teeth; shorter ramus of antennule usually projecting by $\frac{1}{3}$ to $\frac{1}{2}$ its length beyond rostrum.

L. adpersus.

Rostrum usually with 3 ventral teeth; shorter ramus projecting usually by more than $\frac{1}{2}$ its length beyond rostrum.

L. adpersus var. *fabricii*.

Distribution in British Isles.—Bell described the species under the name of *P. leachii* from specimens taken in Poole Harbour. Mr. J. Omer Cooper has kindly sent me a collection of prawns from this estuary, which proved to be made up as follows:—

<i>L. serratus</i>	528
<i>L. adpersus</i>	9
<i>L. squilla</i>	5

It is evident that *L. adpersus* is by no means an abundant species. Mr. Kemp has recorded it from two localities in Co. Galway, in one of which it occurs in company with *L. squilla* and *L. serratus* as it does at Poole, and he notes that it has been taken also at Weymouth and in the Thames estuary. I have myself taken two small specimens from between tide-marks at Burnham-on-Crouch, and have had others sent to me from West Mersea, where it is known as the "Mud Prawn," and is taken in some numbers by eel-catchers. It is an estuarine species, preferring a muddy bottom, but Mersea seems to be about its northern limit, as I have not found it in the Stour or the Orwell, and it certainly does not occur in Breydon Water in Norfolk, where conditions would seem to be favourable.

4. LEANDER LONGIROSTRIS Milne Edwards. (Text-fig. 3.)

P. longirostris M. Edwards, Hist. Nat. des Crustacés, ii. 1837, p. 392.

P. edwardsi Heller, 1863.

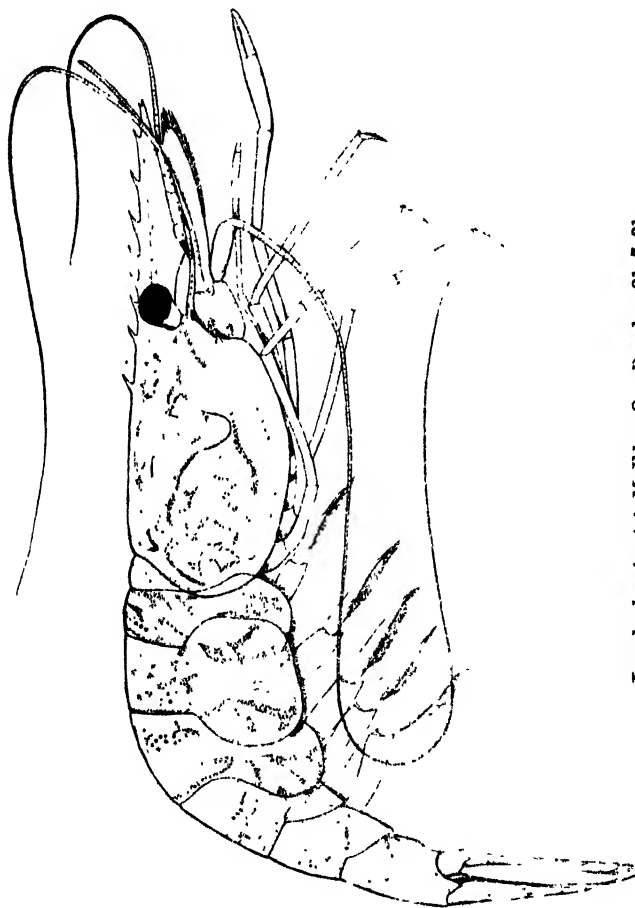
L. longirostris De Man, 1916, p. 149.

There has been some confusion in the use of the name *L. longirostris*, since not only did Milne Edwards describe two distinct species under the same name, but, by a misplacement of a footnote reference, even the authority of the name was wrongly referred to Say. Milne Edwards himself corrected his second

P. longirostris to *P. styliferus*, which applies to an Indian prawn, but Miss Rathbun is undoubtedly right* in maintaining that the name *L. edwardsi* Heller must give place to *L. longirostris* of M. Edwards.

Colour.—The colour is rather variable, but the majority are,

Text-figure 3.



Leander longirostris M. Edw., ♀. Breydon, 21. 7. 21.

in life, almost colourless, and of an opaque white immediately after death. A close examination shows that the whole body, including the rostrum, is speckled with small red chromatophores. In certain areas these chromatophores are surrounded by a halo of blue pigment, which may sometimes be greatly developed and

* Proc. U.S. Nat. Mus. xxvi. p. 50 (1903).

entirely obscure the red. In such cases, which are rare, the animal appears of a very dark purple-black colour. Occasionally the red pigment alone is present, the blue being suppressed, such specimens appearing of a beautiful rosy colour, the margins of the abdominal segments being more deeply coloured. An unusually large female (75 mm.) of this type was taken in the River Bure in July 1922, and has lived in a fresh-water aquarium for over three months without losing its red colouring. There is a tendency for the chromatophores to become arranged in more or less conspicuous lines and patches (text-fig. 3), but these do not give the appearance of distinct bands as in *L. squilla* and *L. serratus*. The limbs are usually colourless, except for a few scattered red chromatophores, but there is sometimes a faint blue colour on the chelæ.

Length.—Female (bearing eggs) 50 to 77 mm. Male 35 to 77 mm. Usually much smaller than the female.

Rostrum.—The rostrum projects considerably beyond the antennal scales, and is deep and nearly straight, but commonly slightly upcurved. It is usually armed with 8 dorsal and 4 ventral teeth, the dorsal teeth being rather prominent, as in *L. squilla*. The first two teeth are situated behind the eye, the third just in front of the orbital notch. As has been pointed out by De Man, it is particularly characteristic of this species that the space between the first two teeth is one-and-a-half times as great as that between the second and third. The following figures show the variation in the number of rostral teeth in 191 females from Norfolk:—

Dorsal teeth:	10	9	8	7
Individuals:	2	18	108	61
	1.04 %	9.4 %	51.3 %	31.9 %
Ventral teeth:	6	5	4	3
Individuals:	2	6	167	16
	1.04 %	3.14 %	87.4 %	8.4 %

In Norfolk, therefore, the usual formula is $\frac{8+1}{4}$, but De Man found the usual formula for Dutch specimens to be $\frac{7+1}{4}$ and that the dorsal teeth varied from 12 to 6. I have excluded males from my table, but have no reason to believe that they differ in this respect from females. The number of teeth does not increase with age or size, and the smaller size of the male is not of itself likely to reduce the average number of rostral teeth. I have not in all cases noted the number of small apical teeth, but in 46 specimens only 3 had two of these teeth, whereas De Man found this number in 42 per cent. The difference may perhaps be explained on the assumption that the proximal apical tooth, when present in Norfolk specimens, is larger and less separated from the others, and has therefore been counted in

with them. On the other hand, the general frequency of occurrence of the various number of teeth differs so greatly that I am of opinion that a real local difference is shown. De Man's figures are as follows:—

Dorsal teeth :	10	9	8	7	6
Individuals :	8 0/0	6.6 0/0	37 0/0	52 0/0	1.3 0/0
Ventral teeth :	6	5	4	3	
Individuals :	1.06 0/0	2.1 0/0	67 0/0	29 0/0	

Mandible palp.—Three-jointed, the second joint about half as long as the third in the adult, but only one-third of it in young specimens.

Antennule.—The short flagellum is two-thirds, rarely a little more, of the length of the peduncle, and is fused to the longer flagellum by about one-third of its length. Taking the average of seven measurements, and regarding the total length as 100, the result is as follows:—Fused part 31; free part 69; the free part being therefore about twice the length of the fused part.

Second leg.—The second leg reaches beyond the antennal scale by the whole of the chela and usually about one-third of the carpus. The dactylus is usually nearly one-third of the length of the whole chela, but the proportion is very variable, and it may sometimes be nearly equal to the palm. The chela of this leg does not therefore provide means for distinguishing this species from *L. adspersus*. The chela exceeds the length of the carpus by about one-tenth, and the carpus is usually slightly longer than the merus. Carpus and merus are, however, so nearly equal that very careful measurement is necessary to determine which is the longer. An average of 20 measurements gave the figures:—Carpus 101; merus 100!

Distribution.—*L. longirostris* has been recorded from Liberia (Rathbun), Corsica, and the French coast at Noirmoutier. It has also been found in the River Gironde as far up as Bordeaux, and in the Loire up to Vertou (30 miles). In the British Museum there are specimens from near Seville, about 50 miles up the River Guadalquivir. De Man found it to be common at certain points on the Dutch coast. In the estuary of the Meuse it is abundant in the Hollandsch Diep, and has been taken as far up as Werkendam, which is just above the Biesbosch. It occurs also in the Zuider Zee, the IJ, in the Rhine near Katwijk, and in the Scheldt up to Antwerp. It therefore inhabits estuarine regions, but within the range of sea-water. De Man only records *L. squilla* from the outer Scheldt on the Zeeland coasts, so that it seems to be replaced in Holland by *L. longirostris*.

In Norfolk this prawn is abundant in Oulton Broad, and in Breydon Water at certain times, and it is known to local fishermen as the "Jack Shrimp" or "White Prawn." In Oulton it is used as bait for perch-fishing, but not for food. In Breydon it is said to be more numerous when there is much fresh water passing

down, but it is found in abundance, at all events in the breeding-season, even when the water is entirely salt. On the other hand, the numbers are generally found to increase towards the upper end of the estuary. It is never taken at sea by the shrimpers, though it is said to be caught occasionally just at the mouth of Yarmouth Harbour. Mr. Patterson has sent me specimens taken at St. Olaves on the Waveney, and probably its distribution is continuous from Yarmouth to Oulton Broad via the Waveney. No doubt it also occurs in the Yare, at least as far as Reedham, but I have not been able to search for it there. In the Bure it is common, probably at all states of the tide, as far up as Acle, 14 miles from the sea, and I have even taken it in Heigham Sounds, 22 miles from the sea. It is well known to the eel-catchers, and numbers are taken in the eel-nets at certain times. At South Walsham eel-set they are usually found in the net after there have been high salt tides in the river and the salt water is beginning to run down again. At such times they are also commonly taken in an eel-set near Hickling Broad.

To judge from its distribution in Norfolk, *L. longirostris* is essentially a river prawn capable of existing either in salt or in fresh water, but preferring that part of the river in which the water is generally brackish. Their indifference to salinity is such that they may be repeatedly transferred directly from fresh water to salt and *vice versa* without any apparent ill-effects, and I have at this moment a number which, taken originally in salt water, have been living for months in pure fresh water. One of these, after hatching her young in salt water in June 1921, was transferred to a fresh-water aquarium in which she moulted 10 days later, and is still (November 1922) flourishing. This indifference to salinity can be equalled by very few animals and surpassed by none.

Breeding.

The fact that, in order to catch *L. longirostris* with certainty and in any numbers, it is necessary to use a trawl either in the lower reaches of the rivers or in Breydon Water, has rather restricted my opportunities for observation, and I have not been able to get representative collections throughout the year. It is, however, certain that breeding begins at the end of May or beginning of June, as it does in *L. squilla*, and that two broods are hatched in the season. A number of specimens taken far up the River Bure on May 16, had ripening ovaries, but no eggs had been laid, but on June 15, 1922, out of 98 females taken in Breydon Water, 48 bore eggs in various stages, 42 had hatched but had not moulted, while 8 had hatched and moulted, and were ready to lay another lot of eggs. All, except one with freshly-laid eggs, had the ovary full. As development probably takes at least a month, and the moult following hatching occurs usually 4 or 5 days later, the first eggs must have been laid this year about May 10. No doubt the larger two-year-old prawns spawn about the middle of May, and are followed towards the

end of the month or in June by the younger females. During June and the first half of July every female taken either bears eggs or can be shown to have hatched young; but about the middle of July, though a large proportion bear eggs, many have evidently ceased to breed. For example, out of 103 specimens taken on July 14 there were 33 with eggs, 46 without eggs, and 24 males. In all the females the ovary was empty.

Egg-bearing females migrate down into salt water as the time of hatching approaches, and, so far as my observations go, the larvæ are very rarely hatched in the river itself. While I have had the larvæ hatch in aquaria in salt water on several occasions, they have never done so when the parent has been kept in fresh or slightly brackish water. In such cases the eggs are eventually stripped off. In more than one case a female kept in fresh water past the time at which the young were expected to hatch has been put directly into salt water, with the result that the young have hatched during the following night. Probably hatching takes place always at night under normal conditions, and the young are carried out to sea by the ebb-tide. I have only once caught a single larva in an early stage of development, in spite of much search in Breydon Water at the height of the breeding-season. A few larvæ in the last stage are occasionally found in Breydon, and doubtless metamorphose there, but the great majority must complete their development at sea and migrate up the rivers in the post-larval condition. Young prawns have been taken 12 miles up the river towards the end of August between 19 and 25 mm. long, but it is by no means easy to obtain these young stages, and it is probable that they are to be found in Breydon much earlier. On the other hand, a very careful search for them on August 28, 1922, in the shallows and among *Zostera*, was entirely unsuccessful, so that it is not improbable that immigration is delayed to a later stage than is the case in *L. squilla*. Mortensen found that the young of *L. adspersus*, though appearing in the shallows about the middle of July, do not reach the innermost parts of certain fjords during the first summer.

Moulting.

The process of moulting takes place usually at night, but I have been fortunate in having been able to witness it on two occasions during the daytime. On each occasion the prawn was found in a peculiar position, the body greatly flexed, the head bent sharply downwards. The cuticle breaks between the thorax and abdomen, leaving the anterior sclerite of the latter attached to the first segment. The thorax then bulges out through the opening, and the animal draws the whole of the thorax and appendages out evenly, without pause. Immediately after freeing the eyes and antennæ, the animal gives a sudden leap forwards, freeing the abdomen instantaneously. The whole process took a

surprisingly short space of time, probably not more than half a minute, but no doubt there were preliminary movements which were not observed. After the moult the movements are most erratic. The prawn may leap about with violent movements of the abdomen or lie on one side in apparent discomfort, moving its appendages continually. Some hours elapse before normal progression is resumed. The very erratic movements immediately after the moult are very likely due in part to the fact that the otocyst is empty, and I was not able to see the process of inserting new grains of sand. The cast skin is often eaten, at least in part, while the newly-moulted prawn frequently falls a victim to its companions.

Breeding females do not, as is commonly the case in *Caridea*, moult immediately after hatching of the eggs. Both this species and also *L. squilla* and *P. varians* moult 4 or 5 days after hatching, but the moult may be delayed even longer. For example a female about 70 mm. long was taken on July 17, the condition of her pleopods showing that she had recently hatched young; but she did not moult till August 19, or 33 days later.

I am unable to say at what intervals adult prawns normally moult, since this can only be ascertained by keeping single individuals for long periods under as nearly as possible natural conditions. Warrington's observations on this point are, in my opinion, quite unreliable, since several prawns were kept in the same aquarium. The female mentioned above moulted a second time on October 5, an interval of 47 days, no growth having taken place. On the other hand, another adult female kept for over a year in fresh water has only moulted once during the whole period.

5. *PALEMONETES VARIANS* (Leach).

Colour.—To the naked eye *P. varians* is generally almost colourless and translucent, except for traces of yellow-orange colour at the end of the abdomen and on the joints of the legs. Under a lens the whole body is seen to be speckled with small blackish chromatophores. On the thorax these are generally arranged in lines, and have a faint yellow halo, while a few pure yellow chromatophores are scattered among them. The rostrum is colourless, except for a row of orange-yellow chromatophores below and of black ones along the middle line. The eye-stalks and antennules are richly pigmented. The abdomen is speckled with black and yellow like the thorax, but there is also an orange spot at the junction of segments 4 and 5, and 5 and 6. The uropods and telson have orange and black spots, but the pleopods are colourless. The chelæ of the second legs have an orange patch at the base and at the end of the dactylus, while a similar patch is seen on the merus of the remaining legs. Barrois* has

* Bull. Soc. Zool. France, xi. (1886).

described the colour of this species, and has drawn attention to the orange colour of the chelæ as a striking character.

Length. Female 29-43 mm. Male 18-25 mm.

Mandible.—Palp absent.

Rostrum.—The rostrum is narrow and straight, or even may be somewhat depressed, and it is armed with a variable number of teeth. I have examined a large number of specimens from Norfolk and from other localities, and find that the formula $\frac{5}{2}$ is by far the most usual. A small apical tooth is present in more than half the individuals. Four or six dorsal teeth are not uncommon, but it is exceptional to find more or less than two ventral teeth. Only one tooth is situated on the carapace behind the eye.

The number of rostral teeth has long been known to be variable, and this variation has been studied by Weldon *, Brozek † and others. The latter has made a statistical study of the numbers of teeth in specimens from various localities in fresh and brackish water, and concludes that the fresh-water form from south Europe has on an average a larger number of dorsal teeth than the brackish northern form. His figures are as follows:—

Plymouth (Weldon)	4·3
Lago di Castello (Italy)	4·9
Skutari	6·4
Montenegro	6·3
Monfalcone (Istria)	5·7

As in a later paper he has given the frequency for 134 specimens from Copenhagen to have been 6·22, there seems to be no ground for supposing that the number of teeth has anything to do with geographical situation or salinity.

It is, however, not improbable that a statistical study of the rostral teeth based on a large material would show constant local variations, since many populations of this species must be isolated for long periods and subject to intense selection. The result is hardly likely to justify the great labour necessary, but it may be of interest to summarize such facts as I have collected bearing on this point (Table II.). The figures given in this table express the frequency of occurrence of various numbers of dorsal teeth as percentages of the individuals examined. It should, however, be mentioned that Weldon's figures alone are drawn from a really adequate material (915 specimens). So far as the figures go, they show that six dorsal teeth is far more frequent on the East Coast and in Scotland than it is at Plymouth, though the examples from the Stour are an apparent exception. The range of variation is also less.

Antennule.—The shorter flagellum is about four-fifths, or

* Journ. M. B. A. n. s. i. p. 469 (1900).

† SB. K. Böhm. Ges. Wiss. Jg. 1907, 1909, and 1912.

between 70 and 80 per cent. of the length of the peduncle, and the fused basal part is almost three-quarters of its total length (between 70 and 75 per cent.).

TABLE II.

Dorsal rostral teeth of *P. varians*.

Number of teeth.

Locality.	Author.	1.	2.	3.	4.	5.	6.	7.
Monfalcone, Istria	Brozek.	..			2	31	57	10
Plymouth	Weldon.	2	2	13	41	38	5	1
Forth Estuary, Scotland	Evans.	5	9	2	9	42	28	2
River Bure, Norfolk . . .	R. G.				20	53	20	7
Wells, Norfolk.....	"		...		15	51	34	
Maldon, Essex	"			...	45	27	27	
Stour Estuary, Suffolk ...	"		...		35	58	6	

Second leg —Reaches, when extended, beyond the antennal scales by the dactylus or part of the dactylus only. The dactylus is about half the length of the palm. The carpus is very long, and greatly exceeds the length of both the chela and the merua.

The Telson.—The form and armature of the telson is very constant throughout the Palæmonidæ, and that of *P. varians* is normally armed in precisely the same way as is that of the British Leanders—namely with two pairs of small spines on the dorsal surface, two pairs of large terminal spines, and a pair of feathered setæ springing from beneath the median triangular prolongation of the telson. There are, in addition, one or two (normally one) small hairs on either side of the projection dorsally.

This arrangement of spines and setæ is very variable in *P. varians* from Norfolk. Out of 30 specimens taken in the River Bure only 17 were entirely normal, three more differed only in having an additional pair of dorsal setæ, and one in having an additional minute ventral seta. The remaining nine were strikingly abnormal in respect either of the number of terminal spines or of ventral feathered setæ, as follows:—

One had only a single feathered seta in the middle line.

Four had three of these setæ.

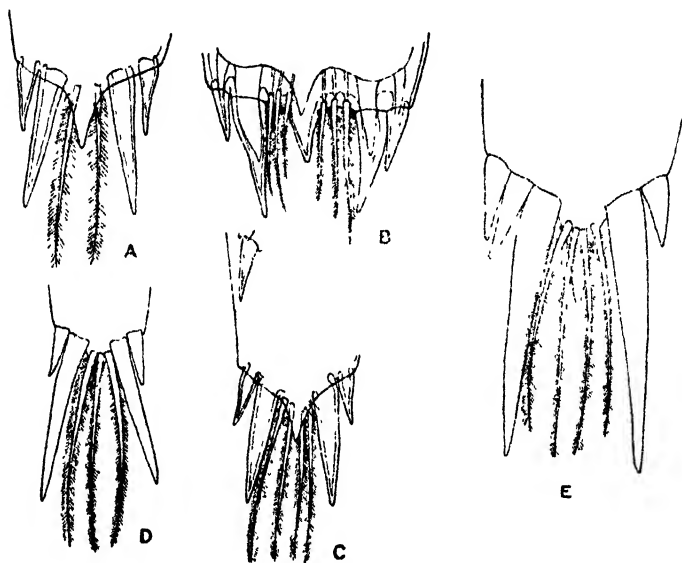
One had four, one had five, and one had six feathered setæ.

One had three pairs of terminal spines.

The specimen with six setæ (text-fig. 4 B) is evidently a case of the retention of the whole of the original seven pairs of larval setæ.

These deviations from the normal are of some interest, since systematic importance has been attached to the numbers of these feathered setæ, and the presence of more than two of them has been given as one of the principal characters of the genus *Allo-caris* Sollaud. It is evident that it possesses neither generic nor specific importance. Pesta* has already shown that Sollaud's genus is untenable on this and other grounds, and states that he has found four setæ in the telson of *P. varians* from Albufera.

Text-figure 4.



Telson.

- A. *Palæmonetes varians* with supernumerary pair of dorsal setæ.
- B. " " " four supernumerary ventral setæ
- C. *P. varians* from Algeria.
- D. *L. squilla* with three ventral setæ.
- E. *L. serratus* with additional spine and four ventral setæ.

I possess specimens from Algeria which likewise all have four setæ.

The frequent presence of supernumerary setæ in *P. varians* is no doubt a primitive character, or perhaps more precisely a retention of a larval character comparable to the non-development of a mandible palp.

In the British species of *Leander* the telson varies very little, but supernumerary feathered setæ are occasionally met with.

* Ann. K.K. Naturh. Hofmus. Wien, xlvii. (1913).

For instance, among 30 specimens of *L. squilla* from Wells one possessed three of these setæ. Among ten *L. serratus* from Poole one was found not only with four setæ, but with an additional terminal spine (text-fig. 4 E).

Distribution.—As is well known, *P. varians* inhabits fresh water in the Mediterranean region and brackish or salt water on the North Sea and Atlantic coasts, but it is not exclusively a fresh-water species even in the Mediterranean region, since it is recorded by Gourret * in salt water in the Étang de Thau and Étang de Berre on the south coast of France, in company with strictly marine species such as *Leander xiphius*.

The distribution has been fully described by Barrois †, but may be briefly repeated here with some additions.

In fresh water it is recorded from several of the Italian lakes, Venice, Dalmatia, Montenegro, Scutari, Corfu, Turkey, Egypt, and Mesopotamia. According to Pesta, *Allocaris sinensis* is only a variety of this species, its distribution being thereby extended to China (Pekin). It has been found in a hot spring at San Giuliano, near Pisa, at a temperature of 28·75° C. In Tunisia it is said to be very common in fresh waters in the south (Gabes, Tozeur, &c.), and has even been found in water at a temperature of 25° to 27° C. I have taken it myself in a stream near Biskra in the Algerian Sahara.

In salt or brackish water it has been found in the Étangs de Berre and Thau (S. France), the Black Sea, Seine Estuary, Boulogne and Pas-de-Calais, coasts of Holland and Friesland, Portugal, Denmark, North Germany and Sweden.

In Britain it is probably widely distributed. It is recorded from several localities on the coast of Devon, Dorset, and Cornwall, and seems to occur all round Ireland. It has also been taken in the Isle of Wight, on the Northumberland and Durham coasts, and by the estuaries of the Forth and Clyde in Scotland.

In Norfolk the great stretch of salt marsh between Thornham and Salthouse is eminently suited to the requirements of *P. varians*. These marshes are seamed with muddy creeks which are empty at low tide, but the marsh between lies for the most part above the level of spring tides. Dotted over this marsh are innumerable small pools full of brackish water, and in almost every one of them these prawns are to be found. Late in autumn the young of the year swarm in these pools, having reached a size of about 20 mm., but in June, when maturity is reached, the numbers have decreased most strikingly, showing a great mortality during winter and spring. When breeding begins, the water in some pools may become almost thick with larvæ, very few of which probably survive even to the post-larval condition, since the available food must be rapidly used up. In two pools at Blakeney examined in June large numbers of larvæ were found together with quantities of the Copepod, *Eurytemora lacinulata*.

* Ann. Mus. Hist. Nat. Marseille, v. (1897).

† Bull. Soc. Zool. France, xi. (1886).

When the same pools were visited again in August all the *Eurytemora* had disappeared, and the numbers of young *Palæmonetes* were far less than of the larvæ previously present.

The marshes are occasionally flooded by exceptionally high tides, which may sometimes occur in early summer. In such cases the young must be washed out to sea and spread about along the coast. If it were not for such floods, every pool would become an isolated unit in which a struggle for existence of extraordinary intensity would operate, and the circumstances would be most favourable for the establishment of local races. How far the population of the various pools are in fact isolated it is difficult to ascertain, but there are pools which are probably not flooded by any but very exceptional tides such as occur at intervals of several years. Probably, however, isolation in this sense rarely, if ever, persists for very long, and the sea carries the larvæ up and down the coast, intermingling the various populations.

Breeding-period, &c.

The breeding-period begins, in Norfolk, about the middle or end of May and ceases about the end of July. Larvæ were first met with this year near Yarmouth on June 16, all being in the first stage and hatched since about four days, as most of them moulted within the next two or three days. On June 17 zoæas, nearly all in early stages, were found in great abundance at Wells, so that about the middle of June may be regarded as the main hatching-season. The records of the Marine Laboratory at Plymouth show breeding to begin there in April and to continue till July. The eggs are carried 5 or 6 weeks before hatching, if I may judge from a single female kept in an aquarium, but probably both the rate of development of eggs and larvæ would be rather more rapid in natural conditions. After July I have not found egg-bearing females, and larvæ in early stages are not met with.

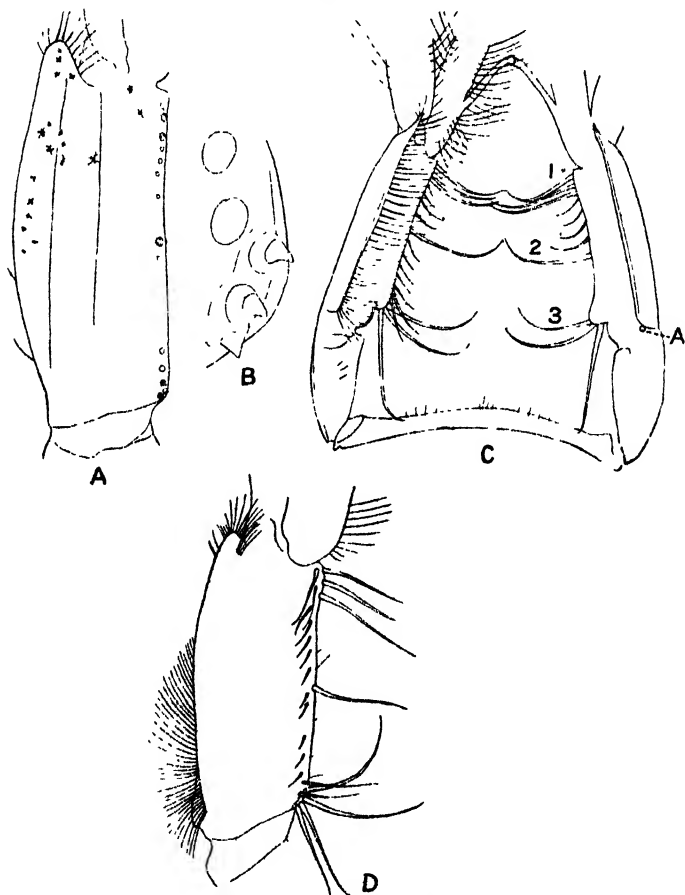
I have not found any direct evidence of females producing a second brood, as is usually the case with *L. squilla* and *L. longirostris*. Examination of large numbers of young taken in September bears out the conclusion that second broods are the exception. That second broods are, however, produced occasionally there can be no doubt, for in some cases the young are found to fall distinctly into two age-groups. For instance, in a pool at Cley on September 6 it was possible to draw a clear distinction between young of 17-22 mm. representing the first brood, and others of 11 mm. or less, some of which were still in the second post-larval stage and must have been hatched about the end of July.

Probably the production of a second brood depends a good deal on local conditions, and is likely not to take place in such small pools, which must be extremely overcrowded, whereas it may be the rule in other and more favourable conditions.

Modification of the Pleopods for egg-bearing in Leander and Palæmonetes.

The pleopoda of the British prawns (I have not been able to examine *L. adspersus* in this respect) are subject to special modification for the purpose of egg-bearing which, so far as I can find, has not been previously referred to.

Text-figure 5.



Second pleopod of female.

- A. *L. squilla* after moult following hatching of eggs.
- B. The same, proximal inner corner more enlarged.
- C. *L. squilla*. Moulded skin after hatching of eggs.
- D. *L. longirostris*. Before laying of eggs.

The condition of the pleopods in the female before and after the breeding-period is shown in text-fig. 5. The shaft or basipodite is broad and flattened on its outer edge into a thin flange, which is either bare or carries a few irregularly-placed setæ. Along the inner face of this joint is a series of circular markings which appear to be spots where the cuticle is thin or pierced by a pore. In the centre of some of them is a short conical projection or spine, and the arrangement of these "spinous discs" is definite and apparently almost constant.

At the moult immediately preceding the laying of eggs a great change takes place. A dense row of feathered setæ appears along the outer side of the basipodite and on its posterior surface, being slightly overhung by the thin outer flange. At the same time, on the inner edge of the joint the place of the "spinous discs" is taken by a series of long, smooth setæ, while a variable number of shorter setæ spring apparently from the remaining circular spots. These long setæ are not the same in number in each pair of legs, but have a remarkably regular arrangement. They may be described as forming three groups as numbered in the figure, while an additional seta may be present on the anterior face in a position corresponding to the letter "A" in the figure, and may be regarded as accessory to Group 3. The following arrangement of these setæ was found in a specimen of *L. squilla*, and may be taken as typical for all the species:—

		<i>Pleopod.</i>				
		I.	II.	III.	IV.	V.
Number of setæ:	Group 1 ...	4	3	3	—	—
	" 2 ...	—	1	1	—	—
	" 3 ...	3	3	3	3	—
	" 3 A ...	1	1	1	1	—

It is to these setæ on the inner face that the eggs are attached, and the outer feathered setæ are no doubt developed partly as a protection to the eggs, and partly to assist in promoting a current of water through them.

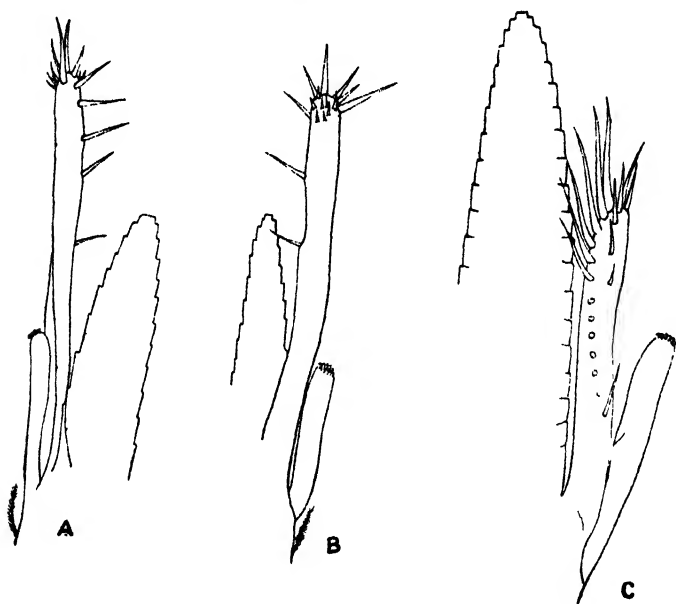
The presence of these ovigerous setæ may be taken as a certain indication that eggs are about to be laid, or that young have been hatched; while their loss marks the end of the breeding-season.

Palæmonetes varians var. *mesogenitor* Sollaud.

The peculiarities in the reproductive habit of the brackish and fresh-water forms of *P. varians* are well known, and "physiological" varieties have been distinguished, namely var. *microgenitor* Boas, var. *mesogenitor* Sollaud, and var. *macrogenitor* Boas, according to the size of the eggs laid and the stage of development at which the young are hatched. These varieties are, however, said to be structurally indistinguishable.

The variety *mesogenitor* Sollaud* occurs in Tunisia, and I have a few specimens, taken in the stream flowing from the Sources D'Oumach, near Biskra, in Algeria, which would probably belong to this variety. They are all small, not exceeding 24 mm., but include four adult males, while the females appear also to be fully grown. While the females differ to some extent from Norfolk specimens in the relative length of the joints of the second leg and the proportions of the short flagellum of the

Text-figure 6.

*Palæmonetes varians.*

A and B. Posterior and anterior views of appendix masculina of two specimens from Algeria.

C. Appendix masculina of specimen from Essex. 34 mm.

antennule, the material is not sufficient to justify any definite conclusion as regards varietal or specific differences. It is otherwise with the males. In all these four males there are two characters which very distinctly separate them from the brackish-water representatives of the species. These are:—

(1) The *appendix masculina* of the second pleopod is slender, and extends by nearly half its length beyond the inner branch of the pleopod. There is a group of strong spines at its apex, but the sides and anterior face are bare or armed with only one or two

* Sollaud, C. R. Acad. Sci. Paris, t. 155, p. 1268 (1912).

spines (text-fig. 6 A, B) In Norfolk specimens (text-fig. 6C) the appendix is always very much shorter than the inner branch of the pleopod, and is provided with a row of spines along the inner and anterior side. This difference is very striking, and easily seen without dissection.

(2) The short flagellum of the antennule is almost or quite as long as the peduncle, and the free part is nearly half as long as the fused part.

TABLE III.

Comparison of measurements of Norfolk and Algerian specimens of *P. varians*.

	SECOND LEG.					ANTENNULE.			
	Dactylus.	Chela.	Palm.	Carpus.	Merus.	Peduncle.	Short flagellum.	"Fused" part.	Free part.
Norfolk, ♂	100	250	150	325	264	100	62	45	17
" ♀	..	269	169	331	254	..	70	49	21
Algeria, ♂	..	267	167	329	236	..	100	64	36
" ♂	96	67	29
" ♀	68	59	9

In all the specimens, male or female, there are either three or four feathered setæ on the telson.

I have not been able to examine any representatives of the South European fresh-water form, and, so far as I know, no attention has previously been paid to these two characters of the male, so that it is possible they may be found to be distinctive not of var. *mesogenitor* alone, but also of var. *macrogenitor*. I consider them of such importance as to justify the separation of the Algerian form as a distinct species, which, if it should prove to be identical with the Tunisian form and not to share its characters with var. *macrogenitor*, should take the name *P. mesogenitor* Sollaud*.

* Since the above was written M. E. Chevreux has been good enough to send me specimens of *P. varians* from Lake Fetzara in Algeria, but unfortunately they proved all to be females. I have also, through the kindness of Dr. W. T. Calman, been able to examine specimens of the var. *macrogenitor* from several localities in south Europe and find that the *appendix masculina* does not differ from that of the brackish-water variety.

10. Report on the Deaths which occurred in the Society's Gardens during 1922. By N. S. LUCAS, M.B., F.Z.S., Pathologist to the Society.

[Received January 26, 1923 : Read February 20, 1923.]

On January 1st, 1922, there were 696 mammals in the Gardens, 1878 birds, and 759 reptiles.

During the year 459 mammals, 1026 birds, and 334 reptiles have been added, making a total for the year of 1155 mammals, 2904 birds, and 1093 reptiles.

Of the 1155 mammals 320 have died, giving a percentage of 27·7.

„ 2904 birds 583 „ „ 20·0.

„ 1093 reptiles 237 „ „ 21·6.

The percentages for 1921 were 21·4, 20·4 and 24·5.

„ „ „ 1920 „ 32·1, 24·3 „ 20·1.

If only those animals are considered which have lived in the Gardens for more than six months 167 mammals have died and 95 reptiles.

This gives a percentage for mammals of 14·4.

„ „ „ „ reptiles „ 8·6.

The percentage for 1921 was 10·0 for mammals.

„ „ „ 1920 „ 16·9

„ „ „ 1921 „ 8·1 for reptiles.

„ „ „ 1920 „ 4·5

For the reasons given last year, it is impossible to give this percentage accurately for birds.

From these figures it would appear that the warm, dry summer of 1921 was distinctly beneficial to the mammals.

It has been felt for some time that the death rate in the unacclimatized mammals has been unduly high. It is hoped that the reservation of a special room in the Sanatorium, where small mammals and birds can be kept under conditions of extra care and attention, will do something to lower the death rate among new arrivals.

It is satisfactory to note that the death rate among the mammals from tuberculosis is still falling. The number of deaths among birds from this disease has risen. This is probably due to the large numbers of birds now in the Gardens. Especially is there crowding in the Western aviary, for of the 31 deaths from avian tuberculosis, 17 have occurred in that aviary. The figures for nephritis still continue low. The two diseases which have accounted for the highest numbers of mammals and birds are congestion of the lungs and enteritis.

Of these, the former represents a state where the lungs contain a great quantity of blood and are darker than normal. They may even reach the stage of being a dull red purple, but they are

still aerated, in contradistinction to pneumonia, where they are consolidated.

The latter represents a state of affairs where the alimentary tract shows various stages of inflammation, varying from bright red to purple, with sloughing of the mucous membrane.

The rarity of pleurisy among mammals referred to in my report for 1920 is still maintained. There have been no cases of this disease in either 1921 or 1922.

Table of Causes of Death.

Causes of Death.	Mammals.	Birds.	Reptiles, etc.	Numbers referring to Notes.
<i>Pulmonary disease.</i>				
Pneumonia	35	30	6	
Congestion of lungs	51	73	22	
Edema of lungs	1	...	
Abscess of lungs	1	...	
Acariasis of lungs	1	
Empyema	2	1
Bronchitis	22	21	6	
<i>Cardiovascular.</i>				
Pericarditis	1	7	1	
Anæmia	2	4	
Ruptured mesenteric artery	1	
<i>Renal disease.</i>				
Nephritis	9	11	2	
Granuloma of adrenal	1	2
<i>Alimentary Tract.</i>				
Abscess of mouth	1	...	1	
Stomatitis	3	
Acute dilatation of proventriculus	2	...	3
Gastritis	3	...	4	
Gastro-enteritis	16	1	16	
Enteritis	50	185	24	
Constipation	1	1	...	
Intussusception	1	4
Gastric ulcer	1	5
Strangulated hernia	1	
Prolapse of bowel	1	
<i>Hepatic.</i>				
Fatty degeneration of liver	4	...	
Cirrhosis of liver	2	1	...	
Necrosis of liver	1	...	
Granuloma of liver	1	
Portal pyæmia	4	...	
Jaundice ? cause	1	1	...	
Tumour of liver ? nature	1	
<i>Pancreatic.</i>				
Pancreatitis	4	
<i>Genital organs.</i>				
Egg-binding	5	...	
Inflamed oviduct	6	...	
Prolapse of oviduct	1	...	
Accidents of labour	3	

Table of Causes of Death (cont.).

Causes of Death.	Mammals.	Birds.	Reptiles, etc.	Numbers referring to Notes.
<i>Nervous System.</i>				
Convulsions ? cause	1	6
Paralysis ? cause	1	7
Delayed shock	1		..	
<i>Acute Infections.</i>				
Tuberculosis	13	31	...	
Mycosis		26	...	
Septicæmia	20	8	3	
General serositis	1	8
Helminthiasis	4	2	3	
Osteomyelitis of jaw	1	9
Peritonitis	1	2	..	
Protozoal infection	1	..	10
Tick infection	1	11
<i>Malignant disease.</i>				
Carcinoma of thyroid	3	12
Sarcoma of liver		1	..	13
Carcinoma of liver	1	14
<i>Disease of Thyroid.</i>				
Adenomatous cyst	1	...	15
Colloid goitre	1	...	16
<i>Miscellaneous.</i>				
Inanition ? cause	1	3	21	
Rickets	3	
Scurvy ?	2	17
Asphyxia	1	...	
Drowned	1	..	
Exposure	1	...	
Killed	19	79	4	
Under anæsthetic	1	
Destroyed by rats	11	1	
Not diagnosed	3	13	12	
Not examined	21	7	25	
Decomposed	14	34	65	

Explanatory Notes on the Causes of Death.

1. One case was that of a hyæna. A sharp piece of bone had perforated the stomach, the diaphragm, and pleura so that the gastric contents had escaped into the pleural cavity.

The other case was that of a Napu mouse-deer.

2. In a rufous-tailed fire-back pheasant.
3. Both of these cases were birds of prey which had over-gorged themselves.
4. In a green cerco pitheque.
5. These were small craterous ulcers in the rumen of a gazelle.
There was also one ulcer in the reticulum.
6. This was in a Caucasian ibex.
7. In a bear.

8. A fishing-cat on post-mortem showed inflammation with exudation of clear fluid in all its serous cavities. It was apparently chronic, as the peritoneum over the liver showed ciliated epithelium.
9. This was a chronic condition in a jungle-cat. The stomach showed extensive secondary ulceration.
10. A sarcocystus infection in a Chinese quail.
11. In a hamadryad.
12. Two of these cases were in wolves and one in a jackal. All showed secondary deposits in the lung.
13. In a hybrid pheasant and Wyandotte hen.
14. In a wolf, apparently primary.
15. In a Cayenne rail. It was spherical and 2 cm. in diameter. It caused death by compression of the thoracic viscera.
16. In a Mandarin duck.
17. In a blackbuck. This had been bred in the Gardens and had produced a young one, which had died a short time previously and shown similar but much less extensive signs of the disease. For a long period there had been no change in the feeding, which seems to have been satisfactory from the vitamine point of view.

11. The Comparative Anatomy of the Tongues of the Mammalia. — VIII. Carnivora. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received November 20, 1922: Read March 6, 1923.]

(Text-figures 15-24.)

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INTRODUCTION.

The materials on which the present paper is based consisted of preserved and fresh specimens in the Society's Prosectorium and the Museum of the Royal College of Surgeons. Nearly five hundred tongues, representative of most genera were examined. Characters were observed which are of considerable value for purposes of classification, and a systematic arrangement of the tongues of the Felidæ, based on these features, agrees closely with Pocock's system (24), which was founded on external and cranial characters. It will be seen that the tongues differ from those described in my papers on the Primates (29), Ungulata, Sirenia, and Cetacea (30). Speaking generally the mechanical power is frequently greater and the gustatory organs are fewer than in many animals already described. The conical papillæ have strong, horny sheaths.

The tongues of the Fissipedia differ in many respects from those of the Pinnipedia.

Suborder FISSIPEDIA.

Section ÆLUROIDES.

The tongue is long and comparatively narrow in all species, but it is wider in *Felis leo*, *F. tigris*, and *F. onca* than in other cats. It thickens progressively from before backwards, but the free part is never very thick. The sides are parallel or tapering, but the tongue is spatular in a few cases. The apex is truncated or rounded, but it is usually devoid of a notch. It is beset with

small conical and fungiform papillæ, but these do not stand up prominently. And there is in no case a large cluster of prominent fungiform papillæ containing large taste-buds, such as are present in the Primates. The *lateral borders* are rounded, but lateral organs are variable. They have many backwardly-directed conical papillæ; these usually lie flat in the Felidæ, but they stand up prominently in some of the Viverridæ. No lobules are present such as occur in the Cetacea.

The oral and pharyngeal parts of the tongue can be easily distinguished from one another when the vallate papillæ form a V or a triangle, and when there is a marked contrast between their conical papillæ. It is, however, difficult to distinguish them when the vallate papillæ form rows which do not meet, and when the conical papillæ maintain the same characters from the apex back to the epiglottis. The papillose base of the tongue is close to the epiglottis in all *Æluroidæ* except *Felis leo* and *F. onca*, in which an extensive, smooth tract of mucous membrane intervenes between the base of the tongue and the epiglottis.

The conical papillæ in the Felidæ, Hyænidæ, and *Proteles*, have thick, sharp or rounded, horny sheaths, which can exert a powerful mechanical action on the food. This character is less marked in many of the Viverridæ. In some of the papillæ in *Proteles cristatus* they form blunt caps for rounded papillæ (text-fig. 21).

Median dorsal sulci and transverse dorsal ridges and sulci are absent. And there is no trace of frenal lamellæ, sublingua, plicæ fimbriatæ, or foramen cæcum.

Circumvallate Papillæ (text-fig. 15). The following patterns are present:--

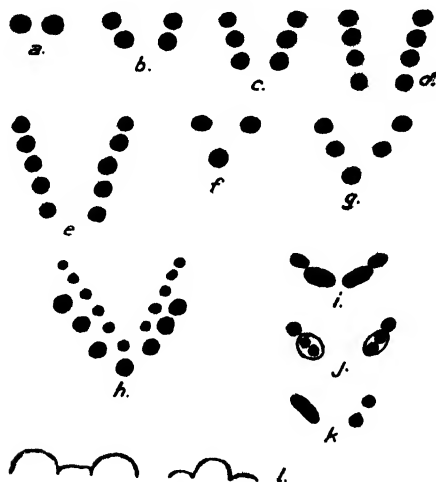
1. A pair of papillæ.
2. Two or more pairs of papillæ arranged in converging rows, which do not meet in an apical papilla.
3. Three papillæ in a triangle with the apex behind.
4. Several papillæ in V-formation.
5. Papillæ form a double V.

The converging rows and the V can be regarded as incomplete or complete chevrons. There is no trace of T or Y types, or of fields of papillæ. And in no case were papillæ absent. It will be seen that pairs of papillæ are present in the Felidæ, Hyænidæ, and *Proteles*, but all types exist in the Viverridæ. As some tongues have no lateral organs, and few fungiform papillæ with taste-buds, the vallate papillæ are frequently the main gustatory organs.

It may be difficult to count the number of papillæ, for they are sometimes very small and inconspicuous, or concealed by overhanging conical papillæ. They may be all equal or unequal in size. They are circular, oval or dumbbell-shaped when viewed from above, and they are cylindrical or conical on elevation. One or more may be included in one fossa. The vallum and

fossa vary in prominence, and the papillary surface is smooth, finely granular or papillated. In the Felidæ, Protelidæ, and Hyænidæ there are one or more pairs of papillæ in rows which converge, but do not meet. In the Viverridæ there are in

Text-figure 15.



The circumvallate papillæ: a-k: papillæ on plan; l: papillæ on elevation.

addition to this pattern three papillæ in a triangle, or several papillæ in a single or double V.

The arrangements seen by myself and recorded by others are:—

Family FELIDÆ.

Felis leo:—One to five pairs of papillæ; seven papillæ in two rows.

F. tigris:—One or two pairs; seven papillæ in two rows.

F. pardus:—One or three pairs.

F. domestica, *F. sylvestris*, *F. caffa*, *F. viverrina*, *F. nebulosa*,
F. bengalensis, *F. concolor*:—Two pairs of papillæ.

F. lynx, *F. caracal*, *F. rufa*, *F. pardalis*:—Three pairs of papillæ.

Cynælurus jubatus:—Two or three pairs of papillæ.

Family VIVERRIDÆ.

Viverra civetta:—Three papillæ in a triangle.

" *fusca*:—Six papillæ in a V.

Civettictis civetta:—Three papillæ in a triangle.

" " Five papillæ in a V.

Viverricula malaccensis:—Three papillæ in a triangle.

Genetta felina:—Four papillæ in a V.

„ *pardina*:— „ „

„ *tigrina*:—Two papillæ on the right side and one on the left.

Hemigale hardwickii:—Three papillæ in a triangle.

„ „:—Four „ „ V.

Paradoxurus larvatus:—Three „ „ triangle.

„ *hermaphroditus*:—Three papillæ in a triangle.

„ *typus*:—Five papillæ in a V.

Mungos mungo, *M. ichneumon* (several examples of each species):—Three papillæ in a triangle.

Atilax paludinosus:—A pair of papillæ.

Nandinia binotata, *Suricata tetradactyla*, *Galidia elegans*:—Three papillæ in a triangle in several examples of each species.

Arctictis binturong:—Eighteen papillæ in a double V (text-fig. 15 h).

Cynictis penicillata:—Three papillæ in a triangle.

Crossarchus obscurus:— „ „ „ „

Family HYÆNIDÆ.

Hyæna striata:—A pair of papillæ (text-fig. 21).

„ „:—Two pairs of papillæ.

H. crocuta:—A pair of papillæ.

Family PROTELIDÆ.

Proteles cristatus:—A pair of papillæ (text-fig. 21).

Fungiform Papillæ:—These are numerous or scanty in the *Æluroidea*; and in some tongues they are well represented, but indistinct. They may stretch right across the dorsum, or they may be absent from the centre, thereby forming a dorsal bounding zone. They are numerous, scanty or absent on the ventral papillary zone. They have the usual arrangement in clusters and rows of varying degrees of obliquity. They are hemispherical or pedunculated, and the surfaces are smooth or granular.

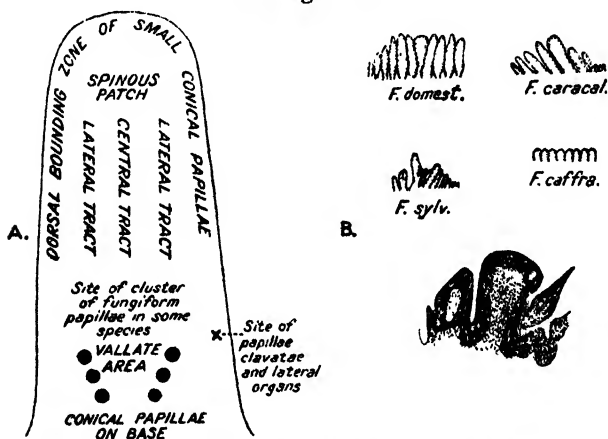
Their distribution on the oral part of the dorsum is determined by the presence or absence, and characters, of the patch of papillæ spinosæ. As a rule they are absent from the latter, but some are present on it in *F. caracal* (text-fig. 20).

In many Carnivora lateral organs are absent, and it is probable that fungiform papillæ lying on the postero-lateral parts of the dorsum replace them. This has been definitely proved to be the case in *Felis domestica*. And it is shown below that club-shaped fungiform papillæ with well-marked taste-buds lie in the position of lateral organs in some Felidæ.

In the Felidæ there may be many fungiform papillæ just behind the apex, but they are never as large and prominent as those in

the Primates. The cluster contains many papillæ in *Felis pardus*, *F. nebulosa*, *F. bengalensis*, *F. concolor*, and *Cynælurus jubatus*. It contains few papillæ in *F. leo*, *F. tigris*, *F. viverrina*, and *F. sylvestris*. No apical fungiforms are present in *F. pardus*. The fungiforms situated along the sides of the oral part of the dorsum also vary. They are absent in some examples of *F. leo*, moderately developed in *F. sylvestris*, *F. pardalis*, and *F. concolor*, and numerous in *F. pardus*, *F. nebulosa*, *F. viverrina*, *F. bengalensis*, and *Cynælurus jubatus*. No papillæ are present in the spinous patch, except in *F. caracal* (text-fig. 20). On the dorsum behind the spinous patch there are insignificant or prominent fungiform papillæ; they are poorly developed in *F. leo*, *F. tigris*, *F. viverrina*, *F. pardalis*, and *Cynælurus jubatus*; they are present

Text-figure 16.



The divisions of the Æluroid tongue (A.) and the characters of the papillæ clavatæ (B.). *F. domest.*: domestic cat; *F. sylv.*: wild cat; a papillæ with a taste-bud greatly magnified is seen in the lower right-hand corner.

in moderate numbers in *F. pardus*, numerous in *F. nebulosa* and *F. caffra*, and very prominent in *F. sylvestris*.

On the posterior parts of the lateral parts of the dorsum there is sometimes a row of finger-like or clubbed papillæ for which I propose the name of papillæ clavatæ (text-fig. 16 A and B). They lie in the position of the lateral organs, and they appear to be modified fungiform papillæ. Histological examination reveals the presence of taste-buds in their epithelium. They are useful for purposes of classification, being present only in *Felis domestica*, *F. sylvestris*, *F. caffra*, and *F. caracal*. Until material comes to hand I am unable to state whether they occur in *F. chaus* and *F. lynx*. They are relatively largest in *F. caracal*.

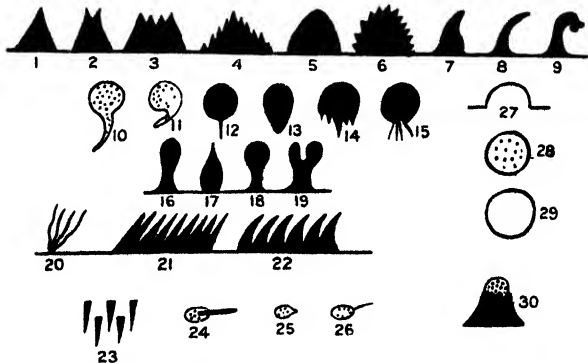
Watson and Young (33) stated that the fungiform papillæ are

numerous in *Hyæna crocuta*. In *H. striata* they are not very numerous.

In *Proteles cristatus* (text-fig. 21) the papillæ form a marked cluster in front of the vallate area, and others are all over the dorsum.

In the Viverridæ the conditions of the fungiform papillæ are more varied than in the Felidæ, for the patch of papillæ spinosæ is absent, weak or strong; and the distribution of fungiform papillæ depends on its characters. In *Nandinia binotata* (text-fig. 21), *Viverra civetta*, and *Civettictis civetta* there is no spinous patch, and fungiform papillæ cover the dorsum from the apex of the tongue to the vallate area, and from one side to the other. A few papillæ are present on the ventral papillary zone. In *Paradoxurus larvatus* the patch is small, and its component conical papillæ are slender; fungiform papillæ encircle it, and a

Text-figure 17.



The lingual papillæ seen under a hand-lens. 1-26: conical papillæ;
27-30: fungiform papillæ.

few are found on it. In other species the arrangement of the fungiform papillæ and the patch are as in the Felidæ.

The characters of the fungiform papillæ are shown in text-fig. 17.

No papillæ clavatæ are present in the Hyænidæ, Protelidæ, and Viverridæ.

The value of the clavate and other fungiform papillæ for purposes of classification is shown on page 149.

Conical Papillæ.—As the mechanical function predominates over all others in the *Æluroidea*, the conical papillæ are strongly developed. And they are provided with sharp-pointed horny sheaths. In the fore part of the oral division of the dorsum there is, in most cases, a patch of large conical papillæ which have been termed papillæ spinosæ; and the area on which they stand is called the spinous patch in this paper (text-fig. 16 A).

The patch may be completely surrounded by a zone of small papillæ, or it may extend laterally till it covers the whole width of the tongue. The histology and chemistry of the horny epithelial sheaths of the papillæ have already been described by Severin (28), Klein and Verson (17), Csokor (7), Podwisotsky (25), and Ranvier (23). The ventral papillary zone may be composed of small conical papillæ alone, or of both conical and fungiform types.

Family Felidæ:—In all forms the spinous patch is surrounded by a zone of small papillæ, but it varies in size, and in the prominence of its papillæ. The points of the papillæ are directed backwards, and are straight or recurved to a variable degree; but those of the papillæ on the encircling zone face backwards and inwards. The lateral papillæ may increase or decrease from before backwards, but the papillæ spinosæ increase in size from without inwards.

In all Felidæ except *F. leo* and *F. onca* the conical papillæ extend back to the epiglottis, but in these species the most posterior papillæ are separated from the epiglottis by a smooth mucous surface. The conical papillæ on the pharyngeal part may be smaller or larger than those on the oral part of the dorsum.

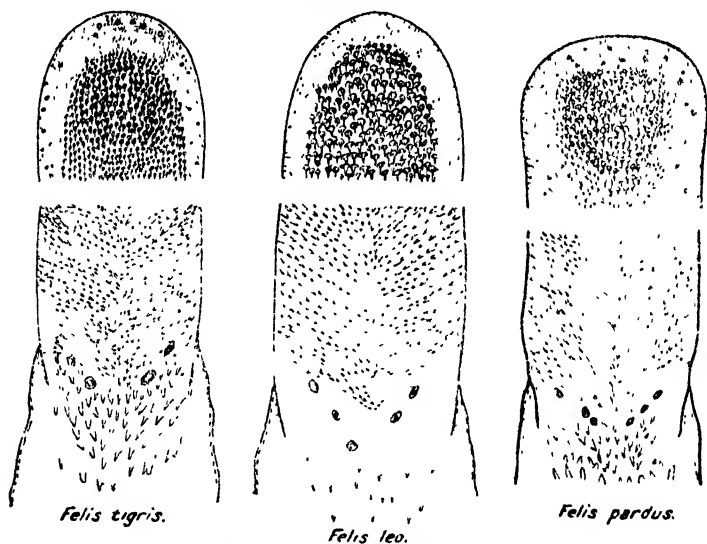
The characters to which special attention must be paid are:—

1. The extent of the small band of conical papillæ encircling the patch of papillæ spinosæ, and the relative quantities of fungiform papillæ situated on it.
2. The posterior limit of the spinous patch, and the distance between the anterior extremity of the patch and the apex of the tongue.
3. The characters of the papillæ spinosæ, particularly the shape of their spines and their closeness or separateness.
4. Characters of the conical papillæ behind the spinous patch.
5. Presence or absence of a row of papillæ clavatæ in the region of the lateral organ on each side.
6. The relative sizes of the conical papillæ on the oral and pharyngeal parts of the dorsum.
7. Character of the ventral papillary zone.

In *Felis leo* (text-fig. 18) the small papillary zone girdling the spinous patch extends back along the anterior third of the tongue. The spinous patch begins close to the apex of the tongue, but does not reach the middle of the oral part of the dorsum. The papillæ spinosæ have sharp, recurved, closely-set points so their bases are not much exposed. Behind the patch the conical papillæ form a central band of small ones and two lateral tracts of large ones. No clavate papillæ are present, and the papillæ on the pharyngeal part of the dorsum are small. In *F. tigris* (text-fig. 18) the conditions are in general similar to those in the lion, but their development is not so great. The papillæ spinosæ have recurved, but not very prominent points, but the conical papillæ on the pharyngeal part of the tongue are prominent. Fungiform

papillæ are more marked behind the spinous patch. The tongue is not separated from the epiglottis by a smooth mucous tract. In *F. sylvestris*, *F. domestica*, and *F. caffra* (text-fig. 20) the zone of small conical papillæ surrounding the spinous patch extends far back along the lateral aspects of the dorsum; it has many fungi-form papillæ at the sides of the tongue, but few behind the apex. The spinous patch begins a considerable distance behind the apex of the tongue, and extends to the middle of the oral part of the dorsum. The papillæ spinosæ are discrete, their points are straight, and their granular bases are visible. Papillæ clavatæ are well-marked. The conical papillæ behind the spinous patch are divisible, according to size, into a central and two lateral

Text-figure 18.

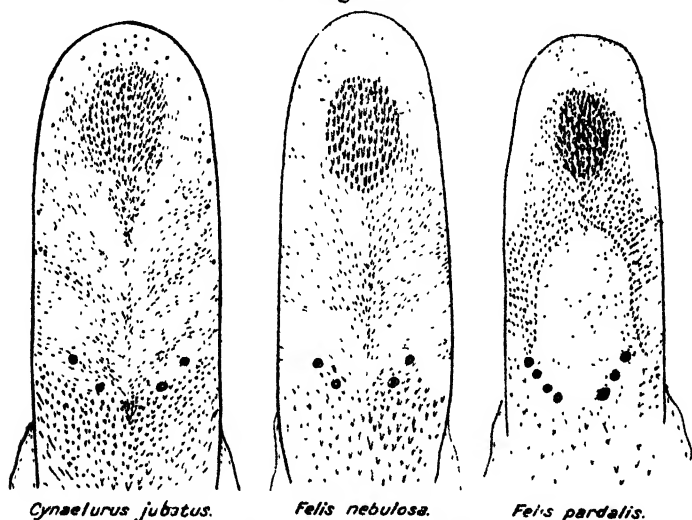


The tongues of the Pantherinæ.

tracts; and the papillæ on the pharyngeal part of the tongue are large. In *F. pardus* (text-fig. 18), of which several varieties were examined, the dorsal bounding zone of small conical papillæ only extends along the apex and anterior third of each lateral aspect of the dorsum; and it is well-studded with fungi-form papillæ; it is also very narrow when compared with the zone on other tongues. The spinous patch begins close to the apex of the tongue, but does not reach the middle of the oral part of the dorsum. The papillæ spinosæ are discrete, and have sharp recurved points. No papillæ clavatæ are present. The conical papillæ behind the spinous patch are divisible into a central and two lateral tracts; and the papillæ on the base of the tongue are

large, soft and not very closely aggregated. The tongue of *F. nebulosa* (text-fig. 19) differs somewhat from that of the last species. The wide dorsal bounding zone of small papillæ contains more fungiforms. The spinous patch begins far from the apex of the tongue and reaches nearer the middle of the oral part of the dorsum. In other respects the tongues are similar. In *F. viverrina* the dorsal bounding zone extends along the anterior third of the oral part of the dorsum: it is narrow and has few fungiforms. Clavate papillæ are absent. The spinous patch begins a short distance behind the apex of the tongue, but lies entirely in the anterior third of the tongue. Its constituent papillæ are slender and inconspicuous. The papillæ behind the spinous patch are arranged in a central and two lateral tracts, and the conical

Text-figure 19.



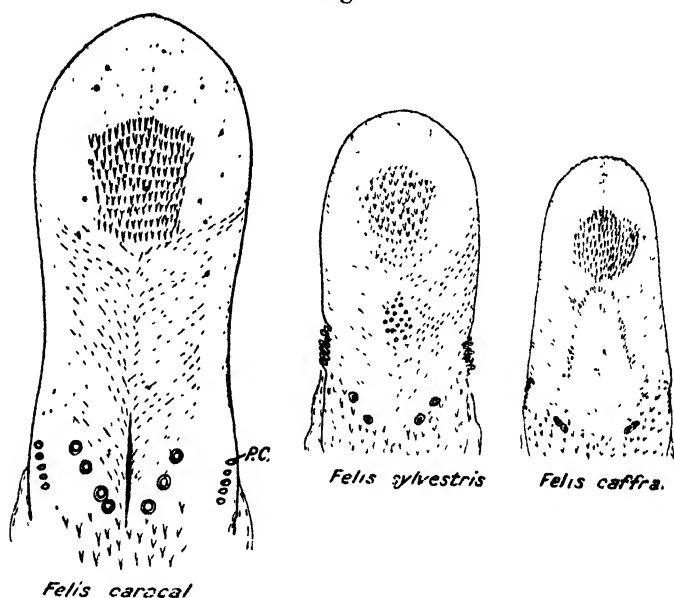
The tongues of the Acinonychiinae and Felinae (No. 1).

papillæ on the base of the tongue are narrow, pointed, and discrete. In the tongue of *F. bengalensis* the dorsal bounding zone is relatively wide and has well-developed papillæ fungiformes. No papillæ clavatæ are present. The spinous patch begins some distance behind the apex of the tongue and extends to the middle of the oral part of the dorsum; its papillæ have strong points. The central and lateral tracts of papillæ behind the spinous patch are just distinguishable; and the papillæ on the pharyngeal part are long, slender, and discrete. In *F. pardalis* (text-fig. 19) the dorsal bounding zone is narrow and has few fungiform papillæ. The spinous patch does not extend as far back as the middle of the oral part of the dorsum. In other respects it is similar to

that of *F. bengalensis*. In *F. caracal* (text-fig. 20) the bounding zone is wide. The spinous patch is small, and begins far from the apex of the tongue. The conical papillæ behind the patch are divisible, according to size, into a central and two lateral tracts. Papillæ clavatæ are very well marked, and form a row of discrete, prominent structures. The conical papillæ on the base of the tongue are pointed and discrete, being separated by wide areas of the pharyngeal part of the dorsum.

In *Cynelurus jubatus* (text-fig. 19) the bounding zone extends half-way back along the dorsum, and it lodges a few small fungiform papillæ. The spinous patch begins far from the apex,

Text-figure 20.



The tongues of the Felinæ (No. 2).

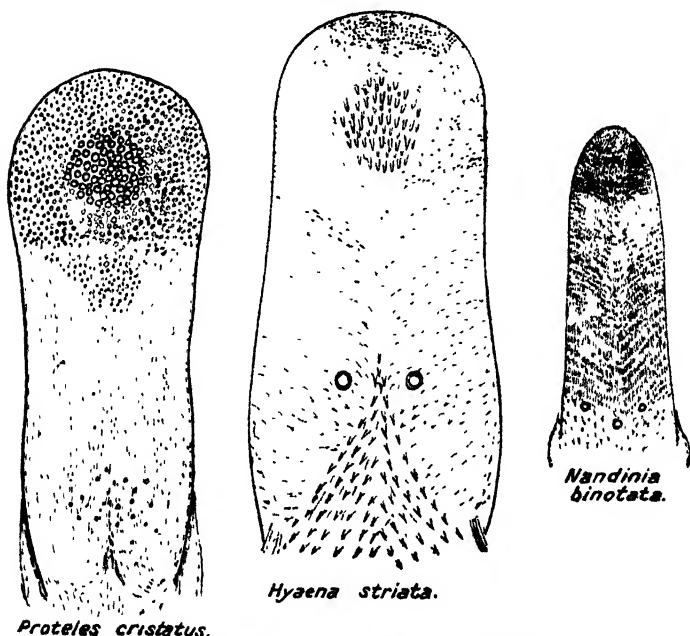
and does not reach the middle of the dorsum; and the points of the papillæ spinosæ are slender and sharp. No papillæ clavatæ are present. The conical papillæ behind the spinous patch are divisible into a central and two lateral tracts, and the conical papillæ on the base are small.

It is, therefore, evident that the tongues of the Felidæ are divisible into two groups, according to the presence or absence of papillæ clavatæ. In the former are *Felis domestica*, *F. sylvestris*, *F. caffra*, and *F. caracal*. As no examples of *F. chaus* and *F. lynx* have come to hand the above list cannot be regarded as complete.

In the latter are *F. leo*, *F. tigris*, *F. pardus*, *F. pardalis*, *F. onca*, *F. serval*, *F. viverrina*, *F. bengalensis*, and *Cynelurus jubatus*. The subdivision of the Felidæ by other characters is given on page 149.

Family Hyænidæ:—In *H. striata* the dorsal bounding zone of small papillæ is wide. The spinous patch begins far from the apex, and is less extensive in proportion to the length of the tongue than that of any of the Felidæ; the points of the papillæ spinosæ are small. The division of the conical papillæ behind the patch into central and lateral tracts is not perceptible. The

Text-figure 21.



The tongues of the Hyænidæ, Protelidæ, and Viverridæ (No. 1).

conical papillæ on the base of the tongue are divided into a central band of large elements, and two lateral tracts of small ones. No papillæ clavatæ are present (text-fig. 21).

Family Protelidæ:—The tongue in *Proteles cristatus* is spatular, and the spinous patch covers the whole anterior expanded part (text-fig. 21). The papillæ on the patch are circular or blunt-pointed cones. The conical papillæ behind the patch are very small and are not divisible into central and lateral tracts. Basal conical papillæ are scanty, and no papillæ clavatæ are present.

Family Viverridæ:—The spinous patch is absent, small or well-

developed, and the development of the points varies as shown in the following table:—

Species.	Development of patch.	Development of points.
<i>Civettictis civetta</i>	—	—
<i>Viverra civetta</i>	+	+
<i>Viverricula malaccensis</i>	++	+
<i>Genetta felina</i>	++	+
„ <i>tigrina</i>	++	+
<i>Paradoxurus larratus</i>	+	+
„ <i>hermaphroditus</i>	+	+
<i>Arctictis binturong</i>	+	+
<i>Nandinia binotata</i>	—	— (text-fig. 21).
<i>Mungos ichneumon</i>	+	++
„ <i>mungo</i>	++	++
<i>Attilax paludinosus</i>	++	+++
<i>Galidia elegans</i>	++	+
<i>Cynictis penicillata</i>	+++	++
<i>Suricata tetradactyla</i>	+	+
<i>Crossarchus obscurus</i>	++	+++ (text-fig. 22).

The conical papillæ have the usual direction, and increase in size in the usual manner. They usually lie flat on the lateral borders, but they project from them in *Nandinia binotata* and *Mungos ichneumon*. Behind the spinous patch they are not divisible into central and lateral tracts as in the *Felidæ*. The conical papillæ on the base of the tongue are usually small, and they are close together or discrete. They are small and discrete in *Nandinia binotata* and *Viverricula malaccensis*; but they are small and close together in *Mungos mungo*, *M. ichneumon*, *Civettictis civetta*, and *Viverra civetta*. They are large in *Paradoxurus larratus*, *Genetta felina*, *Suricata tetradactyla*, and *Arctictis binturong*.

No papillæ clavatæ are present.

Lateral Organs are poorly developed or absent. Various authors have described them in *Felis domestica* (19, 17, 7, 12, 31), *F. tigris* (19), *F. pardus* (12), *Viverra civetta* (19), *V. fusca* (20), *Genetta tigrina* (22), and *Hyaena striata* (19). In my specimens they were arranged as follows:—

Family *Felidæ*:—Organs absent in *Felis leo*, *F. domestica*, *F. sylvestris*, *F. caffa*, *F. caracal*, *F. bengalensis*, *F. nebulosa*, and *F. pardalis*. They are represented by slight fissures in *F. pardus*, *F. concolor*, *F. viverrina*, and *Cynalurus jubatus*.

Family *Viverridæ*:—Organs absent in all except *Nandinia binotata*, *Viverra civetta*, *Cynictis penicillata*, and *Suricata tetradactyla*.

One or two foliate clefts are present in the *Hyænidæ* and *Protelidæ*.

Glands:—Lymphoid nodules and the orifices of ducts and pits are scanty or absent on the base of the tongue. No apical gland

of Nuhn is present. In the cat mucous glands predominate over Ebner's glands.

Lytta:—The lytta lies in the free part of the tongue close to the apex. It is short, and thick or slender; and it is not of much mechanical advantage. Opper describes its histology, and recapitulates the views of Codronchi, Casserius, and Cuvier as to its nature. It has been described in the cat by Flower (10) and by Ludwig, Prince of Bavaria (18). In *Felis leo* it is three-quarters of an inch long and half an inch thick.

The ventral surface of the tongue is plain. It has a well-marked frenum, and there is frequently no trace of a ventral mesial sulcus and ventral papillary zone.

Section CYNODEA.

The form of the tongue and the characters of the apex and lateral borders are essentially similar to those in the *Æluroidæ*. But mesial dorsal sulci are sometimes well marked.

The *circumvallate papillæ* are arranged in converging lines which do not meet in all specimens examined by myself and recorded by others. They are round or oval on plan, and cylindrical or conical on elevation; the fossa is usually well marked, and the vallum is smooth, granular or lobulated. All papillæ may be equal in size, or the members of a row may vary. In some cases the papillæ are concealed by overhanging conical papillæ. The number of papillæ in my specimens, and those in the Museum of the Royal College of Surgeons are:—

Canis familiaris:—One to six pairs.

Canis lupus:—Two or three pairs.

Canis cinereo-argentatus:—Five papillæ in two rows (31).

Canis aureus:—One pair.

Canis mesomelas and *C. azaræ*:—Two pairs of papillæ.

Canis thous, *C. occidentalis*, *C. jubatus*:—Three pairs of papillæ.

Vulpes vulpes, *V. bengulensis*, *V. leucopus*, *V. fulvus*, *Alopec lagopus*, *Cyon dukhensis*, *Lycan capensis*, and *Nyctereutes procyonides*:—Three pairs of papillæ.

As the number of papillæ is variable in those species of which I was enabled to examine several examples they are useless for purposes of classification.

The *fungiform papillæ* may be very obvious, but they are usually minute, and it may be necessary to employ histological examination to detect their presence. In a specimen of *Vulpes leucopus* I was unable to detect them at all. They have the usual arrangement, but the apical cluster is not prominent. Some are present on the ventral papillary zone. Well-developed taste-buds are present in *Canis familiaris* and *Vulpes vulpes*. Papillæ clavatæ are absent.

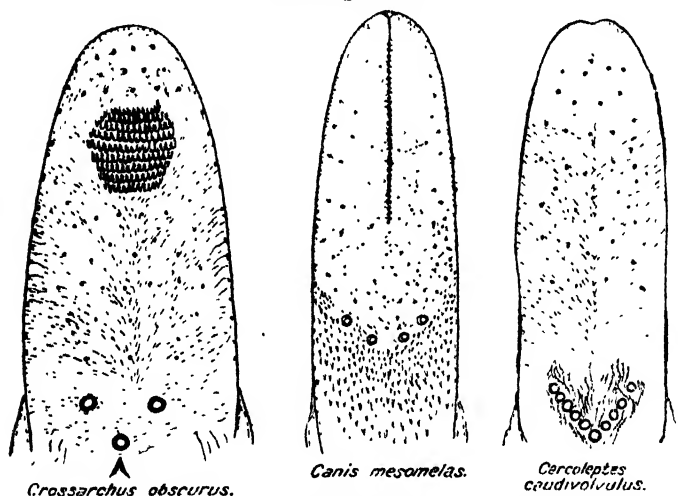
Conical Papillæ:—No spinous patch is present. The papillæ have the usual arrangement in rows and clusters, but those on the oral part are much smaller than those on the pharyngeal

division of the dorsum. A clear line of demarcation, which is concave forwards, separates the two groups. This arrangement was also described in my paper on the tongues of the Lemuroidea (29). The forms are shown in text-fig. 17, 1-6 and 12-15.

Lateral Organs:—Various authors have described them in *Canis familiaris* (23), *C. lupus* (5), *C. cinereo-argentatus* (31), *C. mesomelas* (31), *C. jubatus*, *Vulpes vulpes*, *V. leucopus*, and *V. fulvus*. In *Canis familiaris* they are variable, being present in some specimens, but absent in others. Authors have described the histology of these structures in that species. In the specimens at my disposal I found organs in some specimens of *Canis familiaris*, but not in others.

In the specimens at my disposal I found the organs always very slightly developed when present. No traces were present

Text-figure 22.



The tongues of the Viverridae (No. 2), Canidae, and Procyonidae (No. 1).

in *C. lupus*, *C. mesomelas*, *C. jubatus*, *Vulpes vulpes*, *V. leucopus*, *V. fulvus*. But they were present in all other Canidae enumerated in this paper.

Glands:—In the dog and common fox serous glands surround the vallate papillae and lateral organs, and mucous glands cover the base of the tongue. But there is no apical gland of Nuhn. Lymphoid nodules and orifices of ducts and pits are scanty on the base of the tongue.

The frenum is well marked, but there are no traces of frenal lamellae, plicae fimbriatae, and foramen caecum. The median glosso-epiglottic fold may run forwards for a considerable distance on to the pharyngeal part of the tongue and separate the conical papillae into two groups.

The *lytta* is well developed, and its histological characters have been described by many authors, whose observations have been collected by Oppel (23). In *Canis aureus* it is continued to the hyoid bone by a long, slender fibrous thread.

The characters of the tongues of the Cynoidea are so similar in many species that they cannot be used for purposes of classification, as they can in the case of the *Æluroidea*.

Section ARCTOIDEA.

The tongue is long, narrow and thin. The *apex* is rounded and may or may not have a notch. Notches are absent in the Mustelidæ and *Æluridæ*, but are well marked in some of the Procyonidæ and Ursidæ. Minute conical papillæ clothe the apex, and the fungiform papillæ in that region are small in the Mustelidæ and *Æluridæ*. The apical conical papillæ are long and prominent, but the fungiform papillæ are small in the Ursidæ. The apical fungiform papillæ are large, but the conical papillæ are small in the Procyonidæ. The *lateral borders* are acutely or widely rounded, but lateral organs are variable. The conical papillæ thereon lie flat in the Mustelidæ, *Æluridæ*, and Procyonidæ, but they stand up prominently in the Ursidæ. It was shown in a previous paper (30) that lateral projections are present in *Sus* and the Cetacea. Median *dorsal sulci* are present in many species, but they are very prominent in *Mustela martes*, *M. erminea*, and some species of *Ursus*. Transverse ridges and sulci are very well marked in *Mustela erminea*. The entire dorsum is clothed with papillæ which may be inconspicuous or very prominent, and the conical papillæ on the base may be much larger, or smaller than those on the oral part of the dorsum.

Circumvallate Papillæ:—The following arrangements exist:—

1. One or more pairs of papillæ in two converging rows which do not meet.
2. Several papillæ in V-formation.
3. Several papillæ in a semicircle.

The following list shows the arrangements observed by myself and recorded by others:—

Family MUSTELIDÆ.

Mustela martes:—Two pairs of papillæ.

„ *erminea*:—Three pairs of papillæ in Münch's 27 specimens.

Ictonyx zorrilla:—A pair of papillæ.

Putorius vison:—Two pairs of papillæ in three specimens.

Meles meles:—Seven papillæ in a semicircle (text-fig. 23) or five to nine papillæ in a V.

Arctonyx collaris:—Eight papillæ in a V.

Lutra vulgaris:—Five or eight papillæ in a V.

Mephitis mephitis:—A pair of papillæ.

Conepatus proteus:—Five papillæ in a V.

Galictis vittata:—Eight papillæ in a V.

Family PROCYONIDÆ.

Procyon lotor:—Five pairs of papillæ, or twelve papillæ in a V (text-fig. 23).

Nasua narica:—Four to eight pairs of papillæ in a V (text-fig. 23).

Cercoleptes caudivolvulus:—Ten papillæ in V-formation (text-fig. 22).

Elurus fulgens:—Ten or twelve papillæ in a V (text-fig. 23).

Family URSIDÆ.

Ursus maritimus:—Two pairs of papillæ, or ten papillæ in a V.

„ *arctos*:—16 papillæ in a V.

„ *americanus*:—20 papillæ in a semicircle.

„ *fuscus*:—Ten pairs of papillæ.

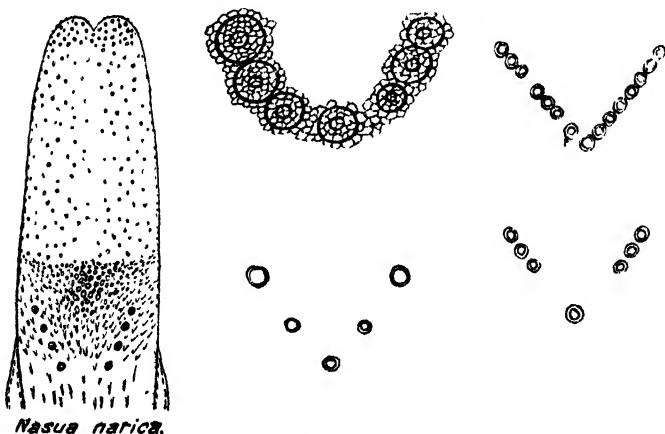
„ *malayanus*:—Seven to thirteen papillæ.

„ *labiatus*:—16 or 17 papillæ in a V.

Melursus ursinus:—Ten papillæ in a V.

The papillæ are round or oval on plan and cylindrical or conical on elevation in all except *Meles meles* in which globular forms are present. The vallum is smooth, granular or lobulated, and the

Text-figure 23.

*Nasua narica.*

The tongue of *Nasua* and the arrangements of the vallate papillæ in the Mustelidæ and Ursidæ.

fossa is closed or patulous. In a specimen of *Meles meles* (text-fig. 23) the mucosa over the papillæ is brown and tessellated; but this appearance was absent in five specimens. The vallums may be in contact (text-fig. 23) or separated by intervals. Numerous taste-buds are present.

The *fungiform papillæ* may be just visible to the naked eye, or

they may stand up prominently. They are inconspicuous in *Mustela erminea*, *M. martes*, and some species of *Ursus*. They are small, but obvious, in *Meles meles*, *Lutra vulgaris*, *Arctonyx collaris*, *Galictis vittata*, *Procyon lotor*, and *Elurus fulgens*. They are larger and more prominent in *Nasua narica* than in any other Carnivore examined by myself. They have the usual arrangement in clusters and rows of varying degrees of obliquity; but they usually stretch from the mid line to the lateral borders of the tongue. Those at the posterior parts of the lateral borders are very prominent in *Cercoleptes caudivolvulus*, and may replace the lateral organs. Taste-buds are present in the fungiform papillæ in many species. Papillæ clavatæ are absent.

Conical papillæ cover the entire dorsum from the apex back to the epiglottis, and they frequently form a ventral bounding zone. But there is no trace of papillæ spinosæ. The conical papillæ have the usual arrangement into apical clusters and rows of varying degrees of obliquity. But their distribution according to size differs considerably as follows:—

1. Papillæ on the oral part of the dorsum large, but those on the pharyngeal part are small:—*Mustela*, *Arctonyx*, *Galictis*.
2. Papillæ on oral part small, but those on the pharyngeal part large:—*Nasua*, *Procyon*, *Elurus*, *Ursus*, *Melursus*, *Ictonyx*.
3. Papillæ small all over:—*Meles*.
4. Papillæ large all over:—*Lutra*.

The papillæ make the edges of the tongue rough in *Mustela*, *Lutra*, and *Nasua*, but the edges are smooth in *Meles*. In *Ursus* they stand up prominently on the apex of the tongue and the anterior ends of the lateral borders.

Lateral Organs:—There is considerable difference of opinion as to their occurrence in the Arctoidea. Various authors have described them in *Mustela martes*, *Putorius vison*, *Procyon lotor*, *Cercoleptes caudivolvulus*, and several species of *Ursus*. I observed no trace of these structures in *Mustela erminea*, *M. martes*, *M. foina*, *Ictonyx zorilla*, *Mephitis mephitis*, *Conepatus proteus*, *Meles meles*, *Lutra vulgaris*, *Procyon cancrivorus*, *Nasua narica*, *Elurus fulgens*, *Cercoleptes caudivolvulus*, *Arctonyx collaris*, *Galictis vittata*. Some small foliate clefts were seen in *Procyon lotor*, *Ursus maritimus*, and *Melursus ursinus*.

There is no trace of frenal lamellæ, sublingua, plicæ fimbriatæ, or foramen cæcum. Lymphoid nodules and the orifices of ducts and pits are scanty on the base of the tongue.

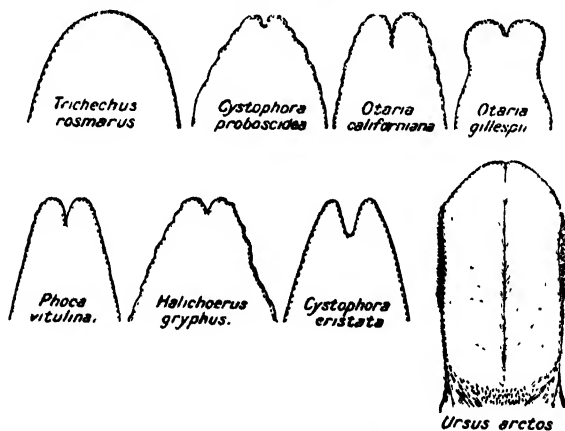
The lytta is present, and it reaches its highest degree of development in *Cercoleptes caudivolvulus*, in which it is long, ligamentous and ensheathed.

Suborder PINNIPEDIA.

The tongues are shorter and wider than those of the Fissipedia, and they taper more rapidly.

The *apex* is entire or cleft, and may be smooth or covered with lobules and papillæ. It is round, massive, smooth, and entire in *Trichechus rosmarus*. In *Cystophora proboscidea* it is rounded, with a deep median cleft, and is covered with coarse lobules. In other forms it has a wide apical sulcus separating its apex into two lateral parts, which vary in appearance. Both halves are covered with papillæ which may be restricted to the apices or extend along the borders. As the specimens examined were not at my disposal for histological purposes I am unable to state whether the papillæ and lobules in the Pinnipedia are homologous with those in the Cetacea and *Galeopithecus*. The halves are rounded in *Otaria californiana*, and they are rounded and laterally projecting in *O. gillespii*. They are sharper in *Phoca vitulina*, *Halichoerus gryphus*, and *Cystophora cristata*.

Text-figure 24.

The tongues of the Pinnipedia and *Ursus*.

The *lateral borders* are rounded in all forms, but are elevated in some examples of *Phoca vitulina*. They are massive in *Trichechus rosmarus* and *Cystophora proboscidea*; they are smooth in the former, but covered with papillæ and lobules in the latter. In other forms they have many small papillæ. In some forms, such as *Otaria californiana*, there are rows of elevations at their posterior extremities, but these must not be mistaken for lateral organs.

Sulci and Ridges.—No ridges are present on either surface. Mesial dorsal and ventral sulci are faint or absent, as in the Cetacea, but transverse sulci were only observed in *Cystophora proboscidea*.

In all forms except *Trichechus rosmarus* the tongue has no intermolar elevation, and the oral part can usually be distinguished

from the pharyngeal division. The former is covered with papillæ in all forms except *Cystophora proboscidea*, and the latter is folded and covered with orifices of glands and pits, as in the Cetacea.

The *circumvallate papillæ* are the chief gustatory organs in *Trichechus rosmarus* and *Cystophora proboscidea*, which have no lateral organs. They are sometimes absent as well, so the gustatory function is poor or absent in some Pinnipedia. The following table shows the arrangement of the papillæ and lateral organs:—

Species.	Circumvallate papillæ.	Lateral organs.
<i>Otaria californiana</i>	Absent.	Absent.
" <i>gillespii</i>	"	"
<i>Trichechus rosmarus</i>	7 in a V.	"
<i>Halichærus gryphus</i>	Absent.	"
<i>Phoca vitulina</i>	5 in a V.	Well marked.
" "	10-12 in a V.	" "
" "	3 in a triangle.	" "
" "	8-9 in a V.	" "
<i>Cystophora cristata</i>	Absent.	" "
" <i>proboscidea</i>	8 in a V.	Absent.

It is, therefore, evident that gustatory organs attain their greatest development in *Phoca vitulina*, and they are poorest in *Otaria californiana*, *O. gillespii* and *Halichærus gryphus*. The conditions are intermediate in *Trichechus* and *Cystophora*.

Fungiform Papillæ:—These are numerous, scanty or absent; and when many are present they are thickly clustered on the centre or sides of the dorsum, or spread all over it. They are hemispherical or pedunculated, and the surfaces are smooth or granular.

Papillæ are absent in *Halichærus gryphus*. They are numerous, especially on the centre of the oral part of the dorsum, in *Cystophora cristata*, but they are aggregated around the edges of the dorsum in *Trichechus rosmarus*. In *Otaria californiana* they are scanty, they stretch right across the dorsum, and they have the usual arrangement. In *Phoca vitulina* the usual mammalian arrangement is present. In the Cetacea fungiform papillæ are absent.

Conical papillæ are absent in *Trichechus rosmarus* and *Cystophora proboscidea*, but they are present in all other forms. And they have their usual arrangement in clusters and rows on the oral part of the dorsum. They also increase in size in the usual manner from before backwards and without inwards. The pharyngeal part is folded and devoid of papillæ standing up from the surface in *Cystophora*, *Phoca*, and *Halichærus*, but large

pedunculated or tapering papillæ are present in *Trichechus*, *Otaria californiana* and *O. gillespii*.

No papillæ clavatæ are present in the place of lateral organs.

Glands:—The orifices may be numerous, scanty or absent. In *Trichechus rosmarus* they are thickly clustered on the oral part of the dorsum, but in other forms they are mainly present on the pharyngeal part.

The frenum is slight or absent, and there are no traces of frenal lamellæ, sublingua, plicæ fimbriatæ, or foramen cæcum.

The ventral papillary zone is narrow in *Otaria* and *Cystophora*.

Tuckerman (31) described how many fat cells are present in the mucous membrane, submucous tissue, and subpapillary zone in *Phoca vitulina*.

No lytta is present in the specimens of *Phoca vitulina* and *Otaria californiana* examined by myself. And the median glosso-epiglottic fold is well marked in the former, but absent in the latter.

The comparisons between the tongues of the Fissipedia and Pinnipedia are shown in the following scheme:—

Suborder FISSIPEDIA:—Tongues long, narrow, thin. Apex entire. Few have laterally-projecting papillæ on margins. Pharyngeal part not folded. Vallate papillæ always present. No gland orifices seen on oral part. Frenum and lytta present. Spinous patch and papillæ clavatæ sometimes present. Lateral organs variable.

Suborder PINNIPEDIA:—Tongue shorter, wider, thicker. Apex cleft in all except *Trichechus*. Edges lobulated or have laterally-projecting papillæ. Mucosa of pharyngeal part folded. Many glandular orifices present. Vallate papillæ frequently absent. Lytta absent. Frenum slight. No trace of a spinous patch or papillæ clavatæ. Lateral organs variable.

SYSTEMATIC.

When the characters described above are arranged in systematic order the following results are obtained:—

Suborder FISSIPEDIA.

Section ÆLUROIDEA.

Spinous patch present in all Hyænidæ, Felidæ, Protelidæ, and most Viverridæ.

Family Felidæ:—Conical papillæ behind spinous patch divided into central and lateral tracts. Patch never reaches edges of tongue. Basal conical papillæ never form a median strip.

Family Viverridæ:—Conical papillæ behind the patch not divided into central and lateral tracts. Spinous patch never

reaches edges of tongue. Basal conical papillæ never form a median strip.

Family Hyenidæ:—Conical papillæ behind spinous patch not divided into central and lateral tracts. Patch never reaches edges of the tongue. Basal conical papillæ form a prominent central strip.

Family Protelidæ:—Conical papillæ behind spinous patch not divisible into central and lateral tracts. Patch reaches margins of tongue. Basal conical papillæ never form a median strip.

FAMILY FELIDÆ.

- A. Spinous patch begins close to apex of tongue, and is restricted to the anterior part of the dorsum. Papillæ spinosæ have recurved points. No papillæ clavatæ.
 - i. Tongue separated from epiglottis by a long, smooth tract of mucous membrane *Felis leo, F. onca.*
 - ii. Tongue not separated from epiglottis by a long, smooth mucous tract.
 - a. Papillæ spinosæ weak *F. tigris.*
 - b. Papillæ spinosæ strong *F. pardus.*
- B. Spinous patch begins close to apex of tongue and reaches middle of oral part of dorsum. Points of papillæ spinosæ recurved and strong. Basal conical papillæ moderately large or small. No papillæ clavatæ.
 - i. Basal conical papillæ moderately long and close *F. jaguarundi.*
 - ii. Basal papillæ small and discrete *F. concolor.*
- C. Spinous patch begins far from apex of tongue. Papillæ spinosæ have strong, straight points. Papillæ clavatæ present.
 - a. Fungiform papillæ on spinous patch *F. caracal.*
 - b. No fungiform papillæ on patch.
 - i. Large fungiforms behind patch *F. sylvestris.*
 - ii. Small fungiforms behind patch *F. caffra, F. domestica.*
- D. Spinous patch begins far from the apex of tongue. Papillæ spinosæ have strong, straight points. No papillæ clavatæ.
 - a. Basal conical papillæ scanty or absent *F. pardalis.*
 - b. Basal conicals long, sharp, discrete *F. viverrina, F. bengalensis.*
 - c. Basal conicals large and close *F. nebulosa.*
- E. Spinous patch begins far from apex of tongue. Papillæ spinosæ have slender points. No papillæ clavatæ. Basal conicals numerous, minute, close *Cynolurus.*

Pocock's classification (24) agrees with the above as follows:—

Subfamily Pantherinæ = Group A.
 „ Felinæ = Groups B, C, D.
 „ Acinonychinæ = Group E.

As regards the Hyenidæ and Protelidæ the characters given at the beginning of this section are all that can be obtained from the tongue for purposes of classification. And the lingual

characters do not show any affinity between *Proteles* and the *Hyænas*. Moreover, they do not show that *Proteles* resembles any of the Herpestine Viverridæ as stated by Weber.

Family VIVERRIDÆ.

A. Spinous patch absent or moderately developed.

a. Patch absent.

- i. Conical papillæ on oral part of tongue strong, but those on base moderately developed *Nandinia*.
- ii. Conicals on oral part small, those on base strongly developed *Civettictis*.
- iii. Conicals on oral part strong, those on base weak or absent *Viverra*.
- b. Patch slight *Paradoxurus*
- c. Patch moderately developed, and its papillæ are nodular *Viverricula*.
- d. Patch moderate, papillæ pointed.
 - i. Vallate papillæ in a single V *Genetta*.
 - ii. Vallates in a double V *Arotictis*.

B. Spinous patch strongly developed.

- a. Points of papillæ sharp *Cynictis, Mungos, Atilax*.
- b. Points broad and blunt *Crossarchus*.
- c. Papillæ globular *Suricata*.

Weber divided the Viverridæ into Viverrine and Herpestine subfamilies. The former corresponds to Group A, and the latter to Group B in the above scheme.

Section CYNOIDÆA.

No trace of a spinous patch in any species. Circumvallate papillæ always in converging rows which do not meet. Fungiform papillæ insignificant. Conical papillæ on oral part of tongue small, but those on pharyngeal part large. Characters so similar in all species that they cannot be used for purposes of classification.

Section ARCTOIDEA.

No spinous patch. No papillæ clavatæ. Fungiform papillæ more obvious than in Cynoidea. Conical papillæ variable.

- A. Conical papillæ on oral part of dorsum large, but those on pharyngeal part small *Mustela, Arctonyx, Galictis*.
- B. Conical papillæ all small from apex of tongue back to epiglottis. *Moles*.
- C. " " " large " " " " " *Lutra*.
- D. " " " on oral part of dorsum small, but those on pharyngeal part large.
 - i. Conical papillæ on anterior ends of lateral borders stand out prominently. *Ursus*.
 - ii. Conical papillæ on anterior ends of lateral borders do not stand out prominently.
 - a'. Fungiform papillæ on posterior parts of lateral borders immense. *Lytta* very large *Cercoleptes*.
 - b'. Fungiform papillæ large all over *Nasua*.
 - c' " " small " " *Procyon, Ailurus*.

Suborder PINNIPEDIA.

- A. Apex entire. Posterior part of tongue elevated. Fungiform papillæ aggregated round edges of dorsum *Trichechus*.
- B. Apex cleft. Posterior part of dorsum not elevated. Fungiform papillæ not aggregated round edges of dorsum.
- a. Halves of apex rounded and blunt. No vallate papillæ nor lateral organs. Large pedunculated conical papillæ on base of tongue *Otaria*.
- b. Halves of apex sharper. Vallate papillæ or lateral organs or neither present. No large pedunculated papillæ on base.
- i. No fungiform papillæ. No vallate papillæ. No lateral organs *Halichoerus*.
- ii. Fungiform papillæ, vallate papillæ, and lateral organs well marked *Phoca*.
- iii. Fungiform papillæ present. Vallate papillæ or lateral organs present *Cystophora*.

It is, therefore, evident that *Phoca* has a fuller complement of gustatory organs than all other Pinnipedia described above.

COMPARISONS WITH THE CETACEA.

It is now believed that the Cetacea have affinities with the Arctoidea and Pinnipedia, so it is necessary to compare the tongues. A full description of the Cetacean tongue is contained in the previous paper of this series (29).

The tongue is long, narrow and thin in the Arctoidea, but wider and thicker in the Pinnipedia and Cetacea. The *apex* is entire in most Arctoidea and all Cetacea, but is deeply cleft in all Pinnipedia except *Trichechus*. The *lateral borders* have papillæ in the Arctoidea; they are lobulated in the Pinnipedia and Odontoceti, but entire in the Mystacoceti. *Vallate papillæ* are present in all Arctoidea, many Pinnipedia, but no Cetacea. *Conical papillæ* are present in all Arctoidea and most Pinnipedia, but they are scanty or absent in the Cetacea. *Lateral organs* are variable in the Arctoidea and Pinnipedia, but they are absent in all Cetacea. The *orifices of glands* are innumerable in the Cetacea, fewer in the Pinnipedia, and scanty in the Arctoidea. The *frenum* is well marked and the *lytta* is present in the Arctoidea, but the former is slight and the latter is absent in the Pinnipedia and Cetacea. The *lingual fat* is well developed in the Mystacoceti, in smaller quantity in the Odontoceti and Pinnipedia, and very scanty in the Arctoidea. The *lingual muscles* are well developed in the Arctoidea and Pinnipedia, but they are poor in the Cetacea.

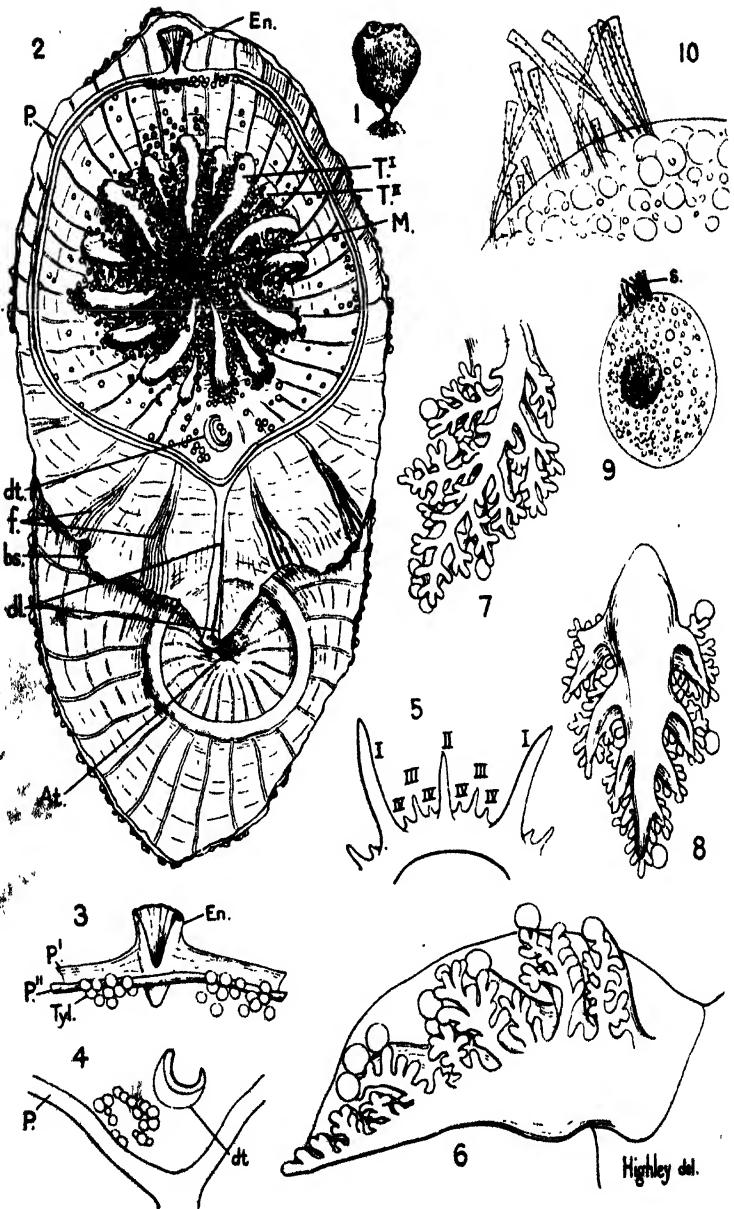
It is, therefore, evident that the tongues of the Arctoidea differ markedly from those of the Cetacea, but the conditions are intermediate in complexity in the Pinnipedia. The conditions in the Cetacea are a mixture of degeneration and hypertrophy. The mechanical and gustatory organs have almost disappeared, but the glands have increased. And the pharyngeal glands are very numerous as well. The secretion of these glands

may contain a viscid or glairy substance which protects the mucous membrane from being injured by prolonged immersion in the water. I also observed numerous pits on the roof of the mouth and on the tongue in fresh-water and marine fishes. But they are not so numerous in the Pinnipedia, as might be inferred from a comparative study of the habits of these groups of animals. Poulton (26) believes that the large glands in the bill of *Ornithorhynchus* secrete a substance which protects the delicate integument. The glands may also be numerous in the Cetacea because salivary glands are absent.

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RHIZOMOLGULA GLOBULARIS PALLAS.

12. Notes on the Tunicate *Rhizomolgula globularis* Pallas *.

By R. KIRKPATRICK, F.Z.S.

(Results of the Oxford University Expedition to Spitsbergen, 1921, No. 24.)

[Received December 1, 1922: Read March 6, 1923.]

(Plate I.)

Among the Tunicata collected by the Oxford University Expedition to Spitsbergen, and sent to the Natural History Museum for identification, were 26 specimens of the small sandy Simple Ascidian *Rhizomolgula globularis* Pallas. As the material is fairly well preserved, the writer believes a few anatomical notes may be of interest.

Description.—The specimens (Pl. I. fig. 1) are somewhat triangular in shape, and covered with fine sand; the largest are about 10 mm. high, not including the stem-like basal process, 10 mm. broad and 3 mm. thick. The two orifices, one at each end of a flat oval area, are usually barely discernible.

Oral tentacles (Pl. I. fig. 2): there are 8 large primaries, 8 secondary, 16 tertiary, and 32 quaternary, *i. e.* 64 in all. Primary tentacles sickle-shaped, compressed laterally.

Dorsal tubercle horseshoe-shaped with opening forwards and to the left.

Branchial folds six on each side, each with five inner longitudinal vessels.

Infundibula deep, with the long double spiral gill-clefts wound in the same direction; accessory gill-slits rather simple, commonly with a single curve nearly flat.

The hermaphrodite sexual gland in the loop of the intestine, the minute oblong kidney, and the paired peduncular secretory glands near the base of the endostyle, all on the left side excepting the right secretory gland.

Locality. Klaas Billen Bay, just above low-tide mark, *i. e.* exposed to the air at low tide; near by a line of large boulders close to the Nordenskiöld Glacier (*C. S. Elton*).

The history of the genus *Rhizomolgula* is interesting. It was founded by Ritter in 1891 for a new species of Molgulid from Prince William Sound, Alaska, 20 fms., *i. e.* outside the Arctic Circle. The generic characters were the existence of the peduncle, the presence of six folds on each side of the branchial sac, the deep infundibula with spiral gill-cleft, and the left-sided position of the intestines and hermaphrodite sex gland, and the

* [This title replaces the title published in the Abstract No. 236.—Ed.]

presence of the peculiar glands supposed to be renal, one on each side of the posterior end of the endostyle. In 1903 Hartmeyer described a second new species, *R. ritteri*, from Baffin Bay, 20 fms.; the new species differed in having fewer inner longitudinal vessels, and in having accessory gill-clefts supposed to be absent in Ritter's species. Hartmeyer showed that the paired glands were not renal, but organs for supplying a secretion for fixing the animal to the bottom; the true renal organ was found by him to be a minute oblong body placed below the stomach.

In 1907-8 Redikorzev described two more new species, *R. gigantea* from Kotelnii Id. and New Siberian Ids., 3-9 metres; and *R. warpachovskii* from Nova Zembla, 40 metres.

In 1908 Michaelsen added a further new species *R. intermedia*, based on some specimens found in the Hamburg Museum, and from an uncertain locality.

In 1911 Huntsman* made the interesting discovery that in 1776 Pallas† had described an undoubted *Rhizomolgula*, viz. *Ascidia globularis* from Kara Sea, and he identifies some specimens from Herschel Id., Canadian Arctic Ocean, with this species.

Lastly in 1916, Redikorzev‡ arrived at the conclusion that all the forms hitherto described belonged to one species, *Ascidia globularis* Pallas, the supposed specific differences being merely variations such as might be found in a large number of specimens from any particular locality; or, again, that certain variations in external appearance (especially as regards the peduncle) might be due to methods of collection and preservation.

The writer adopts Redikorzev's view with the reservation that a more detailed study of the oral tentacles might show genuine specific differences. The number of primary tentacles might be regarded as a specific character, but not the number of multiples of the primary number.

The specimens from Spitsbergen have eight primaries; but there appears to be some uncertainty concerning the number of primaries in the other supposed species [*R. arenaria*, 12-14 tentacles; *R. ritteri*, 12 large ones, also with smaller (about 18 in all); *R. warpachovskii*, 12; *R. gigantea*, 18 in three sizes; *R. intermedia*, 40 in three orders].

Distribution. Pallas's original *Ascidia globularis* was gathered in 1770 from Kara Bay, Kara Sea. Over 130 years later the same species (named *R. warpachovskii* Redkrzv.) was got from Matochkin Strait, Nova Zembla, practically the same locality; for Nova Zembla curves round Kara Sea like a sickle separated from the mainland only by another island. The species is recorded also from New Siberia and from two American Arctic

* Trans. Canadian Inst. 1911-21, ix. p. 127; also Contrib. Canadian Biology, Ottawa, 1912, p. 136.

† Reise, 1776, iii. p. 709, Appendix; and Nova Acta Acad. Petropol. 1787, ii. p. 247, Tab. vii. figs. 39, 40.

‡ Faune de la Russie et des pays limitrophes, 1916. Tunicata, livr. i. pp. 126-137.

localities (Baffin Bay and Herschel Id.), all within the Arctic Circle; and from a place in Alaska outside that circle. The material from Spitsbergen fills in a gap in the circumpolar distribution.

Depth. Shallow water to 40 metres.

There are present in all the examples examined numerous specimens of a species of parasitic protozoa of the group *Suctorio* with a globular sessile body 0.5 to 0.1 mm. in diameter and with one or more tufts of granular slender, vase-shaped tentacles (Pl. I. figs. 2-4, 9, 10).

When the Ascidian is cut in half transversely and the front half turned back, the *Suctorio* appear—under a lens—like snow-balls scattered over the tentacles (fig. 2). They are distributed over the anterior aspect of the tentacles and front wall of the peripharyngeal groove, and never on the posterior wall or the area behind it; they are especially abundant near the upper end of the endostyle and dorsal lamina. This curious distribution led the writer into mistaking the *Suctorio* for sensory organs of the Ascidian, and he has to thank Dr. W. T. Calman for suggesting that the “knobs” were probably parasitic Protozoa.

In 1894 Dr. R. Gottschaldt (Jennische Zeitsch. Bd. xxviii. p. 343) described and figured *Suctorio* found behind the tentacles of the Ascidians *Polyclinopsis haeckeli* Gottsch. and *Synoicum turgens* Phipps from Spitsbergen. The Suctorian figured by Gottschaldt differs from the present one in having knobbed tentacles. Dr. Gottschaldt regards his species as symbiotic rather than parasitic, because the remains at least of the sucked-out Protozoa brought to the Ascidian fall to the lot of the latter; whereas some of the ciliated Infusoria might, in the absence of the *Suctorio*, have escaped altogether.

EXPLANATION OF PLATE I.

Figures of *Rhizomolgula globularis* (Pallas).

- Fig. 1. A rather large specimen. Nat. size.
 Fig. 2. Anterior part reversed, of a specimen cut across transversely, showing the posterior aspect of the tentacles. *T*₁, primary tentacles; *T*₂, secondary; *M*, mouth; *At*, atrial opening; *P*, peripharyngeal bands and groove; *dt*, dorsal tubercle; *dl*, dorsal lamina; *En*, endostyle; *f*, folds of branchial sac; *bs*, cut edge of branchial sac. $\times 10$.
 Fig. 3. Groups of *Suctorio* on or near the anterior peripharyngeal band, near the end of the endostyle. *En*, endostyle; *P'*, posterior pharyngeal band; *P''*, anterior ditto; *Tyl*, the knob-like *Suctorio*. $\times 18$.
 Fig. 4. Group of *Suctorio* in epibranchial area near dorsal tubercle, *dt*. $\times 18$.
 Fig. 5. Part of tentacular ring and tentacles of four orders (mainly diagrammatic). $\times 30$.
 Fig. 6. Primary tentacle, antero-lateral aspect. $\times 60$.
 Fig. 7. Primary tentacle, posterior aspect. Partly diagrammatic. $\times 40$.
 Fig. 8. Primary tentacle, anterior aspect. Partly diagrammatic. $\times 40$.
 Fig. 9. A Suctorian, with a nearly central nucleus-like body, and one tuft of sensory hairs. $\times 280$.
 Fig. 10. Part of a Suctorian. $\times 1400$.

13. On the Feet and Rhinarium of the Polar Bear
(*Thalarctos maritimus*). By R. I. POCKOCK, F.R.S.,
F.Z.S.

[Received February 20, 1923: Read February 20, 1923.]

(Text-figure 1.)

The fore feet resemble in a general way those of all the northern species referred to *Ursus* and *Euarctos* in having a single small isolated carpal pad entirely surrounded by hair and separated from the plantar pad. The pads of the hind foot are very similar to those of the fore foot, but the digitals are a little smaller and the plantar a little larger, although of the same width. A point in which the hind foot of *Thalarctos* differs from that of all other genera of Ursidae is the extent to which the metatarsal area is overgrown with hair, reducing the metatarsal pad to a small elliptical pad occupying nearly the same position as, and only a little larger than, the carpal pad of the fore foot. In the other genera the metatarsal area is either wholly naked or is merely invaded on the inner side by a narrow tract of hair along the groove marking the division between the plantar and metatarsal pad. As subsidiary differences it may be noticed that the carpal pad is altogether smaller, and the plantar pads of both fore and hind foot shorter, than in the rest of the genera.

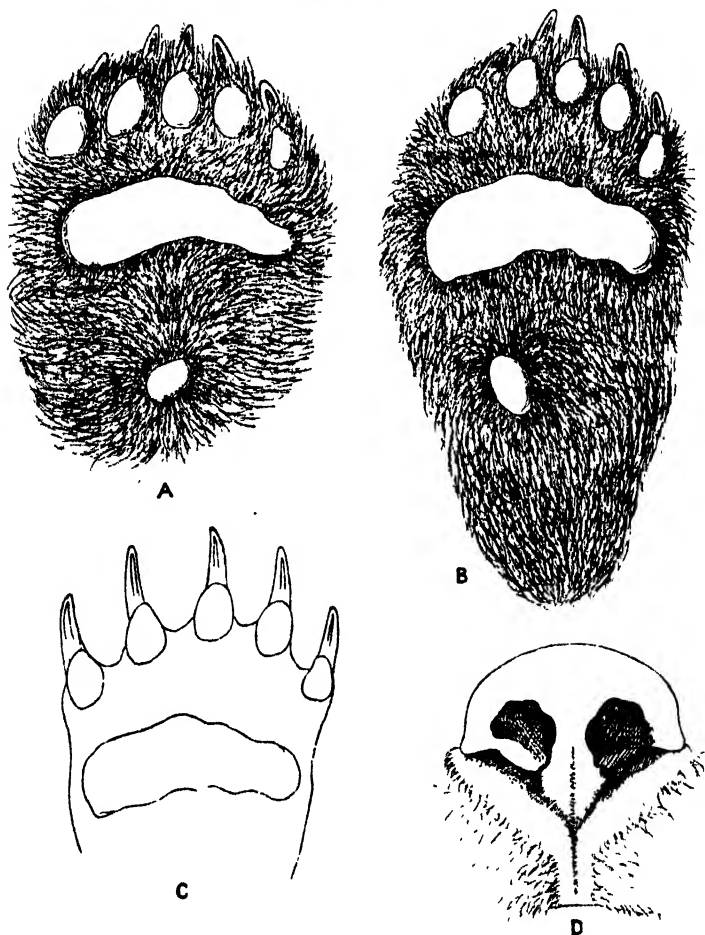
The digits of both fore and hind foot are separable by tolerably equal spaces as in *Ursus arctos*, and, as in that species, the interdigital integument extends approximately half-way along the digital pads.

The rhinarium resembles closely that of *Ursus arctos*, *horribilis*, *Euarctos americanus*, and *Selenarctos tibetanus*. It is everywhere sharply circumscribed by hair, though less so on the upper lip than above. In profile view the internarial septum is not concealed by the lateral border of the nostril; and there is a deep, smooth infranarial area on each side, marked by a shallow groove which diverges outwards and upwards from the middle line to the nostril. Their point of union in the middle line is crossed by another shallow groove, which descends vertically from about the middle of the internarial septum to the ill-defined philtrum, dividing the hairs of the upper lip.

The ears are in no respect degenerate, and resemble those of

Ursus and *Euarctos* in having well-developed supratragus and basal ridges, with a narrow notch between the angular tragus and the much less prominent antitragus*.

Text-figure 1.



- A Lower side of right fore foot of *Thalarcos maritimus*.
- B. The same of the hind foot.
- C. Hind foot of the same with hairs omitted to show the separation and interdigital integument of the digits.
- D. Rhinarium of the same from the front.

* For descriptions of the ears, rhinarium, and feet of other Bears, see Proc. Zool. Soc. 1914, pp. 829-841, and Ann. Mag. Nat. Hist. (9) i. pp. 375-384 (1918).

14. The Embryonic Development of the Porbeagle Shark,
Lamna cornubica. By E. W. SHANN, B.Sc., F.Z.S.,
 Biology Master at Oundle School.

[Received November 13, 1922: Read February 20, 1923.]

(Text-figures 1, 2.)

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I. *Recapitulation.*

In 1910 I investigated the anatomy of the advanced embryonic stage of *Lamna cornubica*. My results were published in the Twenty-eighth Annual Report of the Fishery Board for Scotland. Simultaneously with this publication there appeared a much fuller account of the same subject, profusely illustrated, by Lohberger (4). As this author placed an entirely new interpretation upon the anatomy of the alimentary canal, as well as upon the mode of embryonic nutrition, I was desirous of repeating my investigations; I accordingly asked Dr. Williamson of the Scottish Fishery Board, who had supplied my original material, if ever he obtained more embryos of *Lamna* to give me the opportunity of dissecting them. Cases of the capture of *Lamna* embryos are few and far between, and it was not until 1922 that Dr. Williamson was able to comply with my request. In February of this year a female landed at Aberdeen was found to contain four embryos, each measuring about 35 cm. in total length. These embryos, together with the entire oviducts and ovaries of the mother, were placed at my disposal; for which I take this opportunity of thanking Dr. Williamson. One of these embryos was a male, which is of interest as being the first recorded case of the capture of a male embryo of *Lamna*.

As the result of my investigation of the latest material, I am able to confirm Lohberger's observations almost in their entirety; and this despite a strong preconceived scepticism regarding the possibility of his view of the nutritive process, a scepticism which was shared by all the zoologists with whom I had discussed the subject. Briefly, the facts regarding the development of the embryo are as follows:—

The original yolk-sac is absorbed at a very early period, when the embryo measures about 6 cm. Thenceforward the cardiac portion of the stomach becomes filled with semi-solid matter,

which process distends the abdominal wall of the body to an incredible extent. The yolk-stomach so formed was erroneously described by previous writers (including myself) as a yolk-sac. The semi-solid matter is derived from the ovary of the mother and is actually swallowed by the embryo in the uterus. Feeding continues in this manner for a long time, certainly for more than a year, during which time the yolk-stomach continues to *increase* in size (unlike a yolk-sac) until it assumes gigantic proportions. It will be shown that there is a regular increase in the bulk of the yolk-stomach from the embryo of 35 cm. to that of 55 cm. Embryos have been found in the uterus measuring as much as 75 cm. (Pennant, 5); unfortunately, no record is available of the measurements of the paunch, though it is said to be very large.

The smallest free-living specimens of *Lamna* measure 82 cm. (Day) and 87 cm. (Williamson); these, however, have lost all trace of the yolk-stomach, and in external appearance possess in every detail the character of the adult. Birth presumably takes place when the young shark measures about 80 cm. But to what purpose is the great accumulation of food in the stomach put? Certainly it is not used in body-building, for the free-living young are only a few cm. longer than the paunched embryos. It seems possible that the accumulation of nutrient matter in the embryo is used for the expensive purpose of building the reproductive organs, and that the young at birth are already mature*.

Such a condition would be unique among chordate animals; but, indeed, the very mode of nutrition of the embryo is unique. Viviparity among Elasmobranch fishes is by no means uncommon, and three general methods of nutrition are in vogue: either the yolk-sac forms a pseudo-placental connection with the uterine wall; or the latter secretes a nutrient fluid which is absorbed by means of external gill-filaments; or, again, the uterine wall itself produces long secretile villæ which enter the alimentary canal of the embryo by way of the spiracles. From all these recognized methods of embryonic nutrition the condition in *Lamna* forms a fundamental departure; moreover, whereas in other forms the maternal nutriment is used up at once in body-building, here the vast majority of it accumulates in the stomach as a reserve store.

After consulting the "Zoological Record," as well as from conversations with several eminent ichthyologists, I believe that I am now in possession of all the outstanding facts at present known regarding the embryonic development of *Lamna cornubica*. I have attempted in the following pages to arrange these facts in

* At the same time Dr. Williamson, in a letter to me, says: "A female 3 ft. 6 in. long, in October, was immature. Further, a Porbeagle 6 ft. long, in December, appeared to be a male, but it had only a slight indication of the external male characteristics."

logical sequence, and to interpret them in the light of my recent observations.

II. Record of Material.

Table I. contains a record of the captures of all *Lamna* embryos known to me, and in addition of the smallest free-living specimens. It is apparent at the outset that from the time when the embryo has attained a length of 25 cm. down to the time when it is approaching readiness for birth (75 cm.), we have a fairly complete series of records. None of the embryos in this series, however, differs in any important developmental character from

TABLE I.

Index.	Authority.	Month of Capture.	Length (cm.).	Embryos.	
				Number and Sex.	Length (cm.).
A	Swenander.	Jan.	—	2 ?	5.5 6.0
B	Calderwood.	—	—	?	25.0
C	Collet.	Dec.	—	?	29.0
D	Collet.	Jan.	—	2 ?	29.5
E	Swenander.	—	—	4 ?	30.0
F	Shann.	Feb.	150	1 ♂, 3 ♀	35.0
G	Collet.	Feb.	256	4 ?	42.5
H	Lohberger.	—	—	2 ♀	4.28 5.53
J	Shann.	Mar.	—	1 ? ♂	54.4
K	Shann.	—	150	4 ♀	45.4 60.5
L	Shann.	June ?	—	2 ?	47.5
M	Pennant.	—	—	?	70.0 75.0
N	Day.	—	82	(Smallest recorded free-living young.)	
O	Williamson.	Nov.	87		

the others; the period which they represent, in other words, is mainly characterized by growth in bulk. The only record of an earlier phase is that of Swenander (7), who states that the stalk of the original yolk-sac was present as a mere shred in embryos 5.5–6.0 cm. long.

From the fact that the smallest known embryos (A) were obtained in January, and that they measured not more than 6 cm., it may be inferred that fertilization takes place towards the end of the year. In December and January again we find embryos measuring 29.0 and 29.5 cm. (C, D); these have

presumably been in the uterus for just over a year, since it is incredible that they are of the same age as the minute specimens noted above. Allowing for the incompleteness of the record, subsequent measurements bear out this supposition remarkably well. In February the embryos may measure from 35 to 42 cm., while at the end of March we find one measuring 54 cm. The last named is, according to our supposition, well on in the second year of intra-uterine development. The figures obtained for the months of December to March are sufficiently consecutive to rule out the supposition that they represent the lapse of a second year; in which case we may suppose that the rate of growth during this period is more rapid than during the first year, namely, about 8 cm. per month. This estimate of the rate of growth of the embryos during their second year, however, must be treated with caution; for an embryo (L) said to have been captured in June only measured 47.5 cm., which would reduce our hypothetical rate of growth to about 4 cm. per month. The rate of growth during this period is probably liable to variation; indeed, we find differences in length of 12 to 15 cm. between embryos in the same uterus (H, K). On the whole it seems reasonable to infer that the average rate of growth during the second year of intra-uterine development is 5 to 6 cm. per month.

Dates of the capture of the larger embryos (M) are unfortunately lacking; but if growth continues at the rate indicated, we may suppose that they were captured about July and were then about 21 months old. This supposition, when taken with the observed fact that a free-living young specimen (O) was captured in November, seems to indicate that birth may take place in September or October, *i.e.*, approximately two years from conception. In what state the young are born is a matter of conjecture. The Table shows conclusively that the young at birth are not much longer than the largest intra-uterine specimens; moreover, they are approaching maturity, if not already mature. If the young are born with the yolk-stomach still distended it seems unlikely that in their unwieldy condition they could have evaded capture hitherto. Hence the suggestion offered above, namely, that the yolk store is used in building up the reproductive system. It is extraordinarily difficult to believe that the huge paunch is lost in the course of a few months without any apparent effect upon the growth of the young fish.

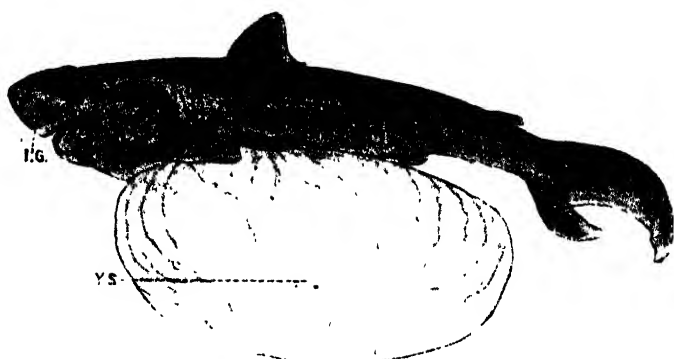
III. *External Features.*

The external features of the advanced embryo are amply illustrated in two earlier papers (Lohberger, 4, and Shann, 6). In order to save trouble in reference to other works, and at the same time to render the descriptions in this paper more readily

intelligible, my drawing of an embryo measuring 454 mm. is reproduced in text-fig. 1. As there is no noteworthy difference in the external features between embryos of 350 to 605 mm., except in point of size, it is possible to make a general summary of the distinctive characters.

In its natural position the cylindrical body is curled around the massive paunch. The snout is extremely blunt and the whole head dorso-ventrally flattened, both of which characters are in strong contrast with the adult condition. There is an internasal groove. The pit beneath the chin shown in text-fig. 1 I now believe to be due to the shrinkage of tissues and not a normal character, for I have not observed it in any other specimen, nor does it appear in Lohberger's excellent photographs. The eyes are well developed. Teeth are prominent in both jaws, even in the smallest specimens examined by me (350 mm.),² but

Text-figure 1.



Embryo of *Lamna*. $\times \frac{1}{2}$.

I.G., internasal groove; Y.S., yolk-stomach (paunch).

they are devoid of the lateral cusps which are found on the teeth of the adult. Vestiges of spiracles are usually, but not invariably, present as minute pores situated midway between the eye and the first gill-slit; in no case yet examined do they communicate with the pharynx. Spiracles in the adult are either absent, or, if present, minute and functionless. The five pairs of large gill-slits are fully open, and the gills well developed (there are no traces of external gills). The lateral line is well marked. The lateral keels, so characteristic of the adult, in the caudal region are prominent, as is the notch in the back at the base of the caudal fin. The cloaca is open. The fins are fully developed and resemble closely those of the adult, excepting the caudal, whose dorsal and ventral lobes have not yet expanded so that they present the chelate appearance seen in the figure (at the

same time the notch on the inner border of the upper lobe is distinctly visible).

The ground-colour is slate-grey fading to cream underneath and upon the paunch. The skin in the younger examples (350 mm.) is perfectly smooth, but in slightly larger ones (430 to 450 mm.) there is a slight roughness due to the developing scales. The skin passes without interruption from trunk to paunch (*i.e.*, without the deep crease which the illustration seems to indicate).

Table II. shows the detailed measurements of a series of embryos. The outstanding feature of this Table is the clear

TABLE II.

(All measurements are in millimetres.)

Index (see Table I.)	F	G	H	K	H	K
Length	350	425	428	454	553	605
Yolk-stomach { long axis	105	185	149	200	211	—
{ short axis	52	—	95	135	123	—
Diameter of Eye	6	—	8	11	12	14
Tip of Tail to Yolk-stomach	—	—	211	—	267	—
Anterior of Cloaca to Root of Tail	95	—	—	100	—	125
Snout to 1st Dorsal Fin	125	—	131	166	178	220
1st Dorsal to 2nd Dorsal Fin	107	—	123	159	178	203
Pectoral to Pelvic Fin	90	—	97	120	131	—
Pelvic to Anal Fin	55	—	53	—	61	—
1st Dorsal Fin { base	25	—	25	44	43	57
{ height	17	—	21	30	32	52
Pectoral Fin { base	20	—	21	26	30	40
{ length	36	47	35	67	54	85
Pelvic Fin { base (transverse)	10	—	10	11	16	21
{ length	20	—	22	29	29	35
Caudal Fin { upper lobe	115	121	115	145	147	168
{ lower lobe	45	54	54	75	82	85

demonstration that the paunch (due to the presence of the yolk-stomach) increases in bulk as the fish grows in size; we are thus forced to conclude that growth at this stage is not due to the use of reserve material, but to some external cause. The other measurements, apart from a few discrepancies (accountable either to normal variation or to individual methods on the part of different observers), give a very fair representation of normal growth.

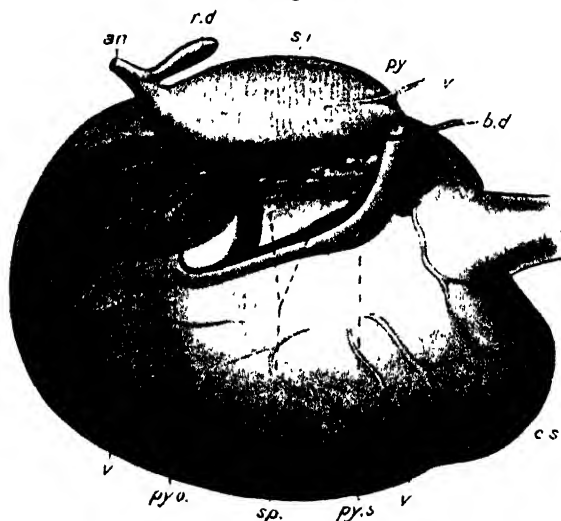
In the male specimen of 350 mm. the claspers of the pelvic fins are manifest even to a casual glance. The fins themselves showed the same measurements as those of the female twin (F).

IV. *Internal Structure.*

A full account of the internal structure of *Lamna* embryos can be obtained by reference to Lohberger (4) and Shann (6); thus it will be necessary here to give only a summary of the outstanding features of the alimentary system, together with certain corrigenda of previous statements. Text-fig. 2 is reproduced from Lohberger to illustrate my description of the alimentary system.

On dissection the outer skin in the abdominal region is found

Text-figure 2.

Alimentary canal of *Lamna* embryo (after Lohberger).

an., anus; *b.d.*, bile-duct; *c.s.*, cardiac portion of stomach ("yolk-stomach"); *oe.*, oesophagus; *py.*, pylorus; *py.o.*, origin of pyloric portion; *py.s.*, pyloric portion of stomach; *r.d.*, rectal diverticulum; *s.i.*, spiral intestine; *sp.*, spleen; *v.*, blood-vessels.

to be underlain by a thin layer of muscle, which is continuous with the lateral muscle of the trunk. The cavity within is a normal coelom. The greater part of the coelom is occupied by the swollen cardiac portion of the stomach, which in an embryo of 350 mm. had a volume of 150 c.c.; it is this organ, in fact, which causes the great ventral distension of the body-wall alluded to above as the "paunch." The wall of the cardiac stomach is richly supplied with blood-vessels. (The statement in my previous paper that the yolk "found its way into every interstice of the dy-cavity, investing completely the abdominal organs" is, of

course, erroneous; it arose through my having been content to dissect a specimen whose stomach had already been punctured.) Anteriorly the cardiac stomach tapers somewhat abruptly to the wide opening of the œsophagus. The latter organ is thick-walled and its lumen is longitudinally ridged; it communicates freely with the pharynx. Leaving the cardiac stomach in the region of the posterior third and slightly on the right side a narrow, but very muscular, tube runs forwards to enter the anterior end of the spiral intestine close to the point where the œsophagus debouches into the stomach. This tube is undoubtedly the pyloric portion of the stomach; it opens by a minute tunnel-like aperture into the cardiac portion, in whose wall it is embedded for some distance. The lumen, though minute, is nevertheless continuous from the cardiac portion to the spiral intestine. The latter organ is fully developed and passes posteriorly into the short rectum, which bears the characteristic dorsal diverticulum. The spleen is well developed (this is the "lobed tissue" whose significance I was unable to determine in my former paper). The pancreas is smaller and does not appear in the illustration, since it is situated on the left side. The liver is of large size and typical shape; it communicates by an apparently functional bile-duct with the apical intestine, entering it from the ventral aspect close to the pyloric opening.

In the youngest specimens examined by me (F) the muscles of the head presented a curious condition. The normal muscles (*e. g.*, constrictor, coraco-mandibularis, coraco-hyoideus, and coraco-branchiales) were recognizable, but instead of being composed of well-defined masses of compact muscle-fibres, the fibres were few in number and embedded in a mass of gelatinous non-cellular material. In older specimens this gelatinous matter gives place to true fibre; the process is correlated with considerable shrinkage in the relative girth of the head of the embryo.

There are five pairs of different branchial arteries, as figured and described by Lohberger. My previous description of six pairs I now consider to have been due to an error in dissection, for I have found only five pairs in the specimens examined since my first dissection was made.

V. *Physiology of Nutrition.*

The cardiac portion of the stomach (yolk-stomach) contains a mass of pale yellow-coloured pulp. The latter is finely granular as seen under the microscope; I failed, however, to find the dumb-bell-shaped granules described by Lohberger. The pulp is not uniform in consistency, for intermingled with it are irregular aggregations of skin-like matter, which Lohberger regards as portions of egg-membrane; indeed, he states that Swenander found two entire egg-capsules in the yolk-stomach of a 30 cm. specimen.

The uterine portion of the parental oviduct is thick-walled and highly vascular; its inner walls, moreover, are thrown into deep folds which have a glandular appearance. There is no evidence, however, that the uterine wall secretes a nutrient material. The uteri of specimens examined by Dr. Williamson contained, as he assures me, no substance apart from the embryos themselves. Swenander (7) found in the uterus of his specimen forty pieces of material, which proved to be groups of eggs surrounded by a common membrane. The portion of both oviducts immediately above the uterus in specimen F contained matter resembling the contents of the yolk-stomach, the lumen of the shell-gland was replete with it, and it was also present in the uppermost portions of the oviducts as far as their source; the skinny content, as might be expected, was not found above the level of the shell-gland. The ovaries themselves were large but contained no ripe ova; their contents much resembled in consistency the matrix in the yolk-stomach, but was darker in colour owing apparently to the accumulation of blood.

Not only did the matter in the yolk-stomach resemble that in all parts of the oviduct as regards physical properties, but a general chemical analysis conducted in the school laboratory revealed no outstanding difference in this respect.

Similar material was found in the mouth and œsophagus of each of the embryos of the F and H groups.

The only conclusion acceptable on this evidence is that nutrient material is derived from the ovary in the form of immature eggs or partially degenerate ovarian tissue—that this is taken up by the oviduct, is partially or completely covered with a thin membrane in the shell-gland, and is passed thence into the uterus, where it is swallowed by the embryos.

The contents of the spiral intestine are of a uniform semi-fluid consistency and of a greenish colour; they have, in fact, every appearance of having undergone the process of digestion. The rectum also contains greenish matter of a somewhat darker shade, and very slight compression of the trunk of the embryo (before dissection) causes this faecal matter to exude from the cloaca.

These observations seem to show that food supplied by the ovary is taken into the alimentary system of the embryo through the mouth and digested in the manner characteristic of free living animals. Owing to the sedentary nature of the embryo there is little wastage of tissue to repair; and, since the supply exceeds the demand, a vast surplus of potential food accumulates in the cardiac portion of the stomach. Whether all the waste products of digestion normally accumulate in the intestine of the embryo until birth, or whether a portion of them is voided into the maternal uterus requires investigation. If faecal matter finds its way into the uterus it must be got rid of in some way. The passage of the uterus to the cloaca is short and wide; it is possible

that water may enter and be expelled through this channel. Such a supposition offers an explanation of why no matter (whether nutritive or faecal) is found as a rule in the uterus on capture. It also offers a solution to the problem of respiration; for, as has been shown, the gills are fully developed and apparently functional. The uterine wall is highly muscular, so that a potential mechanism for pumping water in and out of the uterus is present. Dr. Williamson, in a letter to me, says: "Mr. Ennson observed that the pregnant female dogfishes (piked dogs) when brought up in the trawl had the abdomen distended and sea-water poured out of the cloaca on to the deck."

Although the mode of embryonic nutrition described above, so far as I can ascertain, is unique among Elasmobranch fishes, certain observations by Gudger (3) on the Batoids of Beaufort, N.C., are worth consideration in this connection. Speaking of *Dasyatis say* Gudger remarks:—

"The young are found bathed in a substance of the color and consistence of rich yellow Jersey cream."

"The older embryos had the large intestine filled with a chlorine-yellow substance, evidently the milk-like food secreted by the villi and taken in probably through the spiracles." In the younger stages it is taken in by the long external gill-filaments.

"Notwithstanding the fact that the umbilical cord entered the alimentary tract at the junction of the small with the large intestine, and that the material in the anterior part of the large intestine was lighter in colour than in the middle and hinder regions, it is reasonably sure that it was not yolk." The material is described as "finely divided flocculent grading to large plate-like masses."

In this Ray and in *Pteroplatea maclura* when the uteri are gravid the ovaries are insignificant. The lumina of the ovaries were filled with "an abundant yolky material which probably came from the breaking down of some of the ova."

Gudger does not describe the contents of the upper parts of the oviducts: the question arises, did they contain any of the "yolky material" found in the ovaries? If not, how are we to account for the "large plate-like masses" which were found in the intestine: surely they do not come from a purely milky nutrition? Whether the nutrient matter is taken in through the spiracles (which in a Ray have sufficiently large openings) or through the mouth is a minor consideration; the important point is that food is actually swallowed and digested, according to Gudger, instead of being merely absorbed through gill-filaments. In the Rays, however, the supply does not exceed the demand, and, consequently, no yolk stomach is produced. The fact that in these Rays two batches of young are produced each season precludes the possibility of a protracted intra-uterine development such as occurs in *Lamna cornubica*.

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15. Notes on the Pairing of the Land-Crab, *Cardisoma armatum*. By Miss L. E. CHEESMAN, F.E.S., F.Z.S., Curator of Insects to the Society.

[Received March 5, 1923: Read March 6, 1923.]

As nothing is recorded of the life-history of this species, it was desirable to encourage the pairing of those specimens under observation in the Insect House. Few females, however, have been collected. Of the three consignments of these crabs kindly sent to us by Captain Armitage from the neighbourhood of the mouth of the River Gambia, the first, received in September 1921, consisted of nine males; the second, received in March 1922, consisted of fourteen males, and two small females which died in less than a fortnight. The third consignment, received in July 1922, consisted of thirteen males and two females, one small and one of medium size.

The larger female was placed with a male in a separate bay containing sand and coarse gravel a foot and a half in depth, and a tank of fresh water. The male dug a vertical burrow in one corner, and the female dug a horizontal tunnel in the centre of the bay. The male fed in the daytime, but the female was rarely seen until an hour after closing-time. Both crabs took boiled rice, boiled and raw potatoes, and dry leaves: the male (but not the female) fed also on pieces of raw meat and fish.

In the first week of August the female's tunnel had a second opening on the side nearest the male's burrow, and for the next fortnight they shared the tunnel; neither of the crabs were seen in the daylight during that time, unless disturbed. At the end of a fortnight the male dug a new burrow, and was not afterwards found in the female's burrow.

On August 26th the male was removed, and two tanks were placed in the bay, one of fresh water, the other of sea-water renewed weekly. The female only emerged at night after that date. All the females we have had under observation have been reluctant to show themselves above ground before dusk; this probably accounts for their being less easy to procure than the males. This female came out every three or four nights to feed and bathe, but any movement, or the switching on of the electric lights, caused her to retire to her burrow; if she was out on the other nights she did not feed, for the food was untouched. She was only twice seen in the sea-water tank. If she did not appear for three days the burrow was opened, otherwise she was not disturbed.

On September 18th, 1922, the crab was discovered to be in spawn.

On September 22nd a portion of the eggs was severed from her and sent to Professor McBride at the Imperial College of Science. The crab cast the rest of the eggs that night.

EXHIBITIONS AND NOTICES.

February 6th, 1923.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the months of November and December, 1922:—

NOVEMBER.

The registered additions to the Society's Menagerie during the month of November were 53 in number. Of these 31 were acquired by presentation, 6 were deposited, 8 were purchased, 1 was received in exchange, and 7 were born in the Menagerie.

The following may be specially mentioned:—

1 Cheetah (*Cynalurus jubatus*), from Northern Nigeria, presented by John Holt & Co. on November 21st.

3 Spotted Cavies (*Celogenys puca*), from S. America, purchased on November 17th.

1 Great Kangaroo (*Macropus giganteus*), from Australia, presented by Capt. Daniel and Mr. Urquhart on November 27th.

1 Snowy Owl (*Nyctea scandiaca*), captured at sea, 300 miles from Cape Race, deposited on November 23rd.

4 Searlet Ibises (*Eudocimus ruber*), from South America, purchased on November 20th.

DECEMBER.

The registered additions to the Society's Menagerie during the month of December were 55 in number. Of these 28 were acquired by presentation, 13 were deposited, 11 were purchased, 1 was received in exchange, and 2 were born in the Menagerie.

The following may be specially mentioned:—

1 African Rhinoceros (*Rhinoceros bicornis*), ♀, from Arusha, Tanganyika Territory, purchased on December 15th.

1 Wild Boar (*Sus scrofa*), ♀, and 1 Gmelin's Sheep (*Ovis orientalis*), ♂, from Mesopotamia, presented by Major Dickson, C.I.E., on December 6th.

2 Persian Gazelles (*Gazella subgutturosa*), ♀ ♀, and 1 White-tailed Sea-Eagle (*Haliaeetus albicilla*), from Mesopotamia, presented by Sir Percy Cox, K.C.M.G., K.C.S.I., and Capt. Cheesman, C.M.Z.S., on December 6th.

1 Blue-eyed Cockatoo (*Cacatua ophthalmica*), from New Britain, received in exchange on December 18th.

Lord ROTHSCHILD, F.R.S., F.Z.S., exhibited a fine adult male Mountain Gorilla (*Gorilla gorilla beringeri* Matschie), on behalf of Messrs. Rowland Ward, Ltd. He said:—

“Since my notes on Anthropoid Apes in the P. Z. S. 1904, p. 413, our knowledge of Gorillas has increased considerably. At that time the only material of the Mountain Gorilla was the type-skull, and of the remaining races much more material has come to hand, and it is therefore possible definitely to acknowledge three distinct subspecies, or local races, showing decided structural—especially cranial—differences. Three other so-called species have been separated, but insufficient material prevents any final decision on at least two of these.

“The specimen exhibited, together with a much older solitary male now in the Tring Museum and an adult female, were obtained by Mr. T. A. Barnes at between 6000 and 10,000 feet on the volcanoes near Lake Kivu while collecting butterflies for Mr. J. J. Joicey. In addition to these, there are in England at this moment an adult male obtained by a Belgian officer and an adult male, female, and a baby obtained by the brothers Foster.

“The three following subspecies, or local races, are well defined and distinct:—Gaboon Gorilla (*Gorilla gorilla gorilla* Savage & Wyman); Cameroon Gorilla (*Gorilla gorilla diehli* Matschie); Mountain Gorilla (*Gorilla gorilla beringeri* Matschie). The Gaboon and Cameroon Gorillas, as distinguished from the Mountain Gorilla, are dimorphic, *i.e.* they have a black and a red phase; in the Gaboon race the red phase does not differ in colour on the body, but has the whole crown chestnut rufous, whereas the Cameroon race has a rufous phase in which the red crown is less sharply defined, and the body-colour brown or more mixed with rufous hairs. These rufous phases have been described respectively as distinct species or races as follows: Gaboon race, *Gorilla castaneiceps* Hack., and the Cameroon race *Gorilla gorilla matschiei* Rothsch.; they must, however, stand as *Gorilla gorilla gorilla* form. dimorph. *castaneiceps*, and *Gorilla gorilla diehli* form. dimorph. *matschiei*.

“The Mountain Gorilla is at once distinguishable externally from the two other races by the much stouter and more stocky build, by the much thicker pelage, by the intense shining black of the hair, and by the large fleshy callosity on crest on the top of the head. This crest was first noticed by Mr. Barnes, and his photographs of the animal in the flesh were the first intimation to systematists of this peculiarity. This callosity is similar in its nature to the cheek callosities of the Orang Outan, but unlike these, appears to be common to all adult males, and not a sign of senile impotence as in the Orang.

“The most essential differences of the three races are, however, in the skulls. *G. g. gorilla* has the occipital region narrow and appearing almost triangular, owing to the lambdoidal crest running up to a sharp point in the centre. *G. g. diehli* has the occipital region very broad, and the lambdoidal crest in the

centre only rises to a low blunt point. Lastly, *G. g. beringeri* has the occipital region very broad, and the lambdoidal crest is quite flat and horizontal to support the fleshy callosity.

"The remaining two races *Gorilla jacobsi* Matschie and *Gorilla manyema* (Alix and Bouvier) are more than doubtful, but the material is too scanty to decide definitely. Matschie and Oscar Neumann have definitely applied the name *manyema* to the low country Gorilla of the Congo and, as far as I can see, there are no osteological characters to separate this race from the typical Gaboon race; the two or three adult males examined, however, appear to have the pelage brighter in colour and more sharply contrasted. Of *jacobsi* only the type male is known, and the extremely sharp facial angle of the skull may be an anomaly.

"Adult males of the three well-defined races vary in height from 5 ft. to 6 ft., and there is no specimen preserved over 6 ft. in height, but in the 'Illustration' for February 14th, 1920, p. 129, is a photograph of a gorilla 9 ft. 4 in. in height, according to M. Villars-Darasse, and the photograph certainly shows a gigantic animal. This individual is said to have been killed in the Forest of Bambio, Haute-Lobaze."

MR. OLDFIELD THOMAS exhibited a new Rock-Kangaroo (*Petrogale*) which had been obtained in Northern Queensland by Mr. T. Sherrin, the collector employed on behalf of the Godman Exploration Trustees, by whom it had been presented to the National Museum. It was described as follows:—

PETROGALE GODMANI, THOS.*

General characters about as in *P. assimilis* Ramsay, of which a fine series from Inkerman, N. Queensland, was available for comparison. Black axillary patch less extensive. Forearms more strongly buffy. Tail, instead of being black for its terminal third or half, drabby whitish, its basal fourth only grizzled with black, the rest dull whitish to the end. In a young specimen there was an indication of the upper side being darker, though not so dark as in *assimilis*, but in the adult even this was absent.

Skull of the same length as that of *assimilis*, but it was more convex in the frontal region, and the nasals were decidedly broader and heavier, especially anteriorly, where they had not the marked narrowing found in *assimilis*. Teeth as in *assimilis* except that the secutor was larger, 7-8 mm. in length as compared to a nearly uniform length of about 6-7 mm. in six specimens of *assimilis*.

Dimensions of the type, measured in flesh:—

Head and body 465 mm.; tail 502; hind foot 140; ear 59.

Skull, greatest length 101; condylo-basal length 92; zygomatic breadth 52; nasals, length 41, anterior breadth 8.5, posterior breadth 14.5; teeth, length of i^3 4, secutor 7.8, $ms.^1-3$ 19.

* Abstr. P. Z. S. 1923, No. 235, p. 13.

Hab. North Queensland. Type from the Black Mountain, 16 miles S.W. of Cooktown.

Type. Adult male. B.M. No. 23.1.5, 19. Original number 196. Collected July 20th, 1922, by T. V. Sherrin. Two specimens, adult and young.

This Rock Kangaroo was readily distinguishable from *P. assimilis* by its whitish tail, broader nasals, and larger secator.

Mr. Thomas expressed his pleasure at being able to bring forward so fine a discovery as one of the first-fruits of the Godman Exploration Fund, which had been recently founded by Dame Alice Godman in memory of her husband, Dr. F. Ducane Godman, F.R.S., the well-known naturalist.

The Trustees of the Fund were now to be a permanent body, with their headquarters at the British Museum (Natural History), and would be glad to take charge of any further funds which persons wishing to benefit the National Museum might give or bequeath to them. Such funds would always be administered under the names of, and in accordance with the wishes of, the donors.

Mr. THOMAS also exhibited the skull of a Pygmy Fruit-Bat from Sumatra, upon which he had recently founded a new genus (Ann. Mag. N. H. (9) xi. p. 251, Feb. 1923). The generic name had since proved to be preoccupied, and he therefore now proposed to substitute for it that of *Ethalops*. The type-species would thus bear the name of *Ethalops alecto*.

Mr. J. B. SCRIVENOR, M.A., exhibited, and made remarks upon, a photograph showing the method adopted by Malay natives in breaking in recently-captured Elephants.

Mr. E. G. BOULENGER, F.Z.S., gave an account of his recent visit to Vienna, and of the experiments carried on there by Dr. Kammerer and others upon Amphibians and Insects.

February 20th, 1923.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of January, 1923:—

The registered additions to the Society's Menagerie during the month of January were 156 in number. Of these 55 were acquired by presentation, 15 were deposited, 85 were purchased, and 1 was born in the Menagerie.

The following may be specially mentioned:—

1 Takin (*Budorcas taxicolor*), ♀, from Bhutan, presented by Major F. M. Bailey, C.I.E., F.Z.S., on January 25th.

1 Spectacled Bear (*Tremarctos ornatus*), from the Andes of Peru, presented by H. Fox Strangeways, Esq., on January 16th.

1 Persian Squirrel (*Sciurus persicus*), new to the Collection, from Mosul, presented by Major Dickson, C.I.E.

1 Lesser Niltava (*Niltava macgrigoriz*), from the Himalayas, new to the Collection, presented by E. W. Harper, F.Z.S., on January 24th.

A large collection of N. American reptiles, including 2 Heloderms, 2 Confluent Rattlesnakes, 2 Moccasins, a Copperhead, and a Three-lined Snake (*Atractus trilineatus*), from Trinidad, new to the Collection, purchased on January 25th.

Mr. D. SETH-SMITH, F.Z.S., exhibited a number of skins of Birds-of-Paradise and gave an account of the various forms of sexual display, drawing special attention to the display of the Magnificent Bird-of-Paradise (*Diphyllodes magnifica hunsteini*), a living specimen being now in the Society's collection of tropical birds.

A Cinematograph record of the life-history of the House-fly, taken under the direction of Prof. H. M. LEFROY, F.Z.S., was exhibited.

The SECRETARY exhibited a photograph of the Polar Bears "Sam" and "Barbara."

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of drawings of the feet and nose of the Polar Bear.

March 6th, 1923.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,
in the Chair.

The SECRETARY read the following note from Mr. Caldwell, of the Game Warden's Office, Nairobi:—

"You may be interested to hear of a case of apparent melanism in Tippleskirch's Giraffe, *Giraffa camelopardalis tippelskirchi*. The animal, a bull, was recently seen in the South Game Reserve; its markings are said, by a competent European observer, to have shown through the black in the faint manner that the rosettes show in a black leopard. Wakamba and Masai natives who saw it were much excited, and said they had never seen such a thing before."

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of drawings of the feet and spurs of the Echidna.

In the absence of Sir G. Abercromby, Mr. R. I. Pocock exhibited the mounted head of a Kob from East Africa.

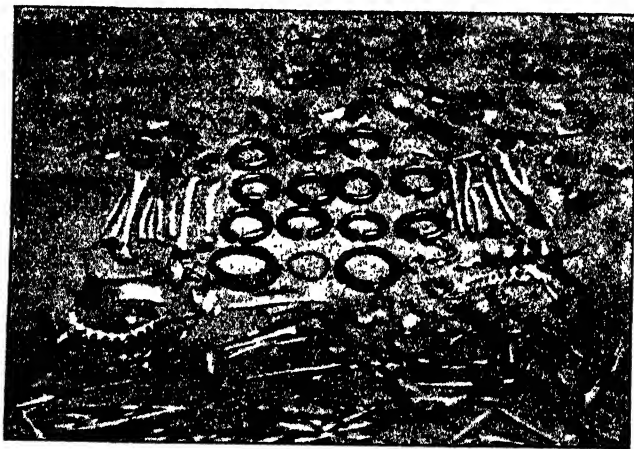
Prof. E. W. MacBRIDE, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of photomicrographs of sections through the nuptial callosities of Frogs of the genera *Rana* and *Alytes*.

Mr. C. F. M. SWYNNERTON, C.M.Z.S., exhibited, and made the following remarks upon, the stomach-contents of a Crocodile:—

"The crocodile, the contents of the stomach of which are shown in the photograph (text-fig. 1), was shot far up the Duma River, flowing into the Speke Gulf of the Victoria Nyanza from the south, on June 6th, 1922.

"Natives came to me to complain of a notorious crocodile, that had taken many people, and, as it was several miles out of my way, I sent a scout to deal with it. According to his own statement, the crocodile made an attempt on himself as he sat beside the water, but, at any rate, he shot it, and it was carried

Text-figure 1.



Stomach-contents of a Crocodile.

whole into my next camp by a large number of natives. It measured only about twelve feet in length, but was of astounding girth. The objects shown in the photograph, all of which were taken by me, or in my presence, from the stomach of this one crocodile, were some heavy rings, some lighter bracelets, a blue bead necklace, a piece of dark cord, the tortoiseshell from the carapace of a tortoise (the bones having apparently been digested first), and the quills of a porcupine (eaten last) and bones. Some of the quills still lay in the crocodile's throat, though most appeared to have been swallowed with the porcupine."

16. On the External Characters of *Elaphurus*, *Hydropotes*, *Pudu*, and other Cervidæ. By R. I. POOCOCH, F.R.S.

[Received February 5, 1923: Read March 20, 1923.]

(Text-figures 2-17.)

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Introduction.

In a paper "On the Specialised Cutaneous Glands of Ruminants" (P. Z. S. 1910, pp. 840-986) I described in some detail these glands in a considerable number of genera and species of Cervidæ, pp. 939 to 967 of the memoir being devoted to this family. Several well-marked forms, however, were not at that time available for examination, *Elaphurus*, *Hydropotes*, and *Pudu* being three of the most important. Since that time examples of *Elaphurus* and *Pudu*, exhibited in the Zoological Gardens, came after death into my hands in the Society's Prosectorium; and the Duke of Bedford, knowing my interest in the subject, very kindly sent to me from Woburn the body of a freshly-killed male example of *Hydropotes*. I am also greatly indebted to His Grace for the chance to examine a second specimen of *Elaphurus*, the body of which he was good enough to send to me. I must also take this opportunity of thanking Major A. Pam, O.B.E., for securing for the Society at my special request the example of the *Pudu* on one of his trips to Chili. To the subjoined account of the external characters of these three rare and isolated genera of Cervidæ, I have added descriptions of some less interesting species which I had not actually examined previously, although the characters of related species belonging to the same genera had been recorded by me. The following paper therefore is supplementary to the one I published in 1910. To facilitate comparison between the two papers, I have in the following pages quoted after each specific heading the page in my previous memoir where the genus or species was referred to.

I have also included in this paper some notes on the rhinarium, ears, facial vibrissæ, and penis, which I did not describe in 1910.

Finally, I must express my regret that, when writing on the glands in 1910, I inadvertently omitted to consult and quote Caton's valuable work on the deer of North America. In this he fully described the glands and other external characters of the species of that country, including those now known as *Rangifer tarandus*, *Alces alces*, *Odocoileus virginianus*, *O. columbianus*, *O. hemionus*, and *O. acapulcensis*, the last-mentioned being regarded at the present time as a subspecies of *O. virginianus*.

To Caton also we owe, I believe, the discovery of the very remarkable fact that in *Odocoileus* the sheath of the penis, instead of being confluent with the skin of the abdomen, so that the short prepuce is situated about halfway between the groin and the umbilicus, is long, pendulous, quite free from the skin of the groin, except at its base, which is close to that of the scrotum.

Genus CERVUS Linn.

CERVUS ELAPHUS Linn. (p. 941).

The feet and glands of a second specimen are identical with those described in 1910.

The rhinarium has the infranarial portion mesially sulcate and slightly narrower than the area between the nostrils; it is not, however, visible in profile view, owing to the forward extension of the hairs of the upper lip. On the upperside the hairs of the muzzle encroach in the middle line some distance beyond the posterior angle of the nostrils. The buccal and ocular vibrissæ are well developed; the interramal tuft is represented by a single vibrissa and the genal tuft by two placed close together and set halfway between the line of the mouth and of the eye, beneath the posterior angle of the latter.

CERVUS CANADENSIS Erxl.

The rhinarium resembles tolerably closely that of *C. elaphus*, except that the upper surface is more overgrown with hair, which extends nearly as far as the anterior border of the nostrils, and the infranarial portion is also narrower, being much narrower than the area between the nostrils, owing to the forward and inward extension of the hairs of the upper lip. (Text-fig. 2, A. B.)

The Asiatic Wapiti (*Cervus xanthopygus*) has a very similar rhinarium.

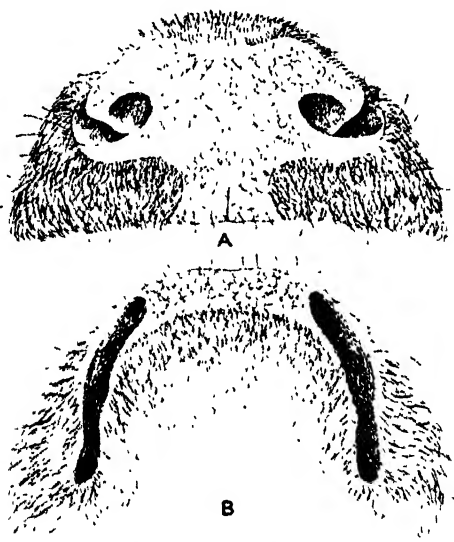
In these two species of *Cervus* the rhinarium is more reduced by hair-growth from the muzzle than in any of the typical deer, except *Dama*, although these genera are surpassed in that respect by *Alces* and *Rangifer*.

CERVUS HORTULORUM Swinh.

As was to be expected, the feet and glands of this species differ in no respect from those of the Japanese species (*Cervus sika*) I described in 1910.

In one example the labial and ocular vibrissæ are normally developed; but the genal and interramal tufts are absent. The rhinarium has a considerable portion of its upper surface, nearly half, overgrown with hairs from the muzzle, which form a convex curve between the nostrils; the infranarial portion is tolerably wide, a little wider than the space between the nostrils. (Text-fig. 3, A.)

Text-figure 2.

A. Rhinarium of Wapiti (*Cervus canadensis*), from the front.

B. The same from above.

Two examples showed an interesting variation in the structure of the penis. In both the urethra was inferior and marked distally by a distinct ridge ending in a slightly upturned point as in other typical Cervine deer; and in one specimen the truncated apex above the urethra was, as usual, lobate, the tips of the lobes folding inwards so as to make a groove where they meet above the point of the urethra. But in the other specimen this terminal portion of the glans was simple and unlobed—a very unusual occurrence. (Text-fig. 17, C, D.)

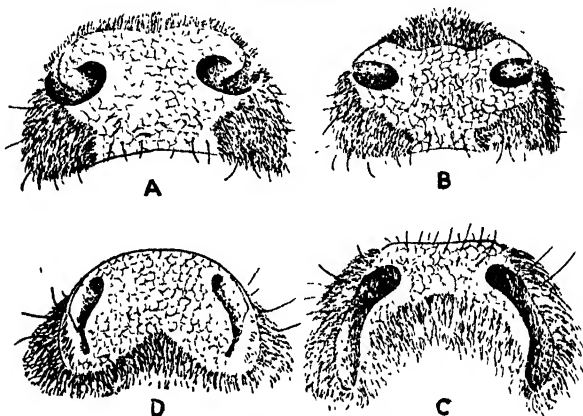
In an example of *C. sika* the glans penis resembled that of the first-described specimen of *C. hortulorum*.

CERVUS ELDI Guthr. (p. 944).

In two additional specimens the feet and glands resembled those of the example described in 1910.

In both specimens the buccal and ocular vibrissæ were well developed. In one of them there was a single long genal and a single long interrampal vibrissa. In the other there were two rather widely separated genals, but no interrampal*.

Text-figure 3.



- A. Rhinarium of *Cervus hortulorum*, from the front.
- B. The same of *Dama dama*.
- C. The same from above.
- D. The same of *Cervus eldi*.

The rhinarium is large. On its upper side the hair of the muzzle advances in the middle as an angular growth, which reaches to a point approximately in a line with the middle of the nostrils. The infranarial portion is wide, considerably wider than the area between the nostrils. (Text-fig. 3, D.)

Genus *Axis* H. Smith.

Axis axis Erxl. and *A. porcinus* Zimm. (pp. 948-950).

Two examples of the Chital or Axis Deer (*A. axis*) examined since 1910 show some interesting variations in the hairiness of the glandular depression on the front of the pastern of the hind foot.

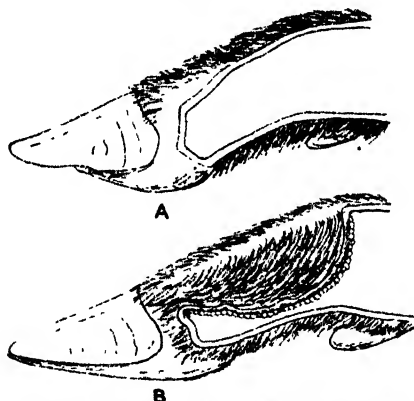
In the specimen originally described the walls of the depression were covered with short, rather sparsely scattered hairs and the

* I have noticed in other species of Cervidæ that the genal and interrampal vibrissæ are of inconstant occurrence within specific limits.

interungual tie was naked. In both the other examples the walls of the depression were clothed with long hairs running downwards and forwards, following the curve of the floor of the pouch, but capable of being raised so as to project from its orifice. In one of these two specimens the interungual tie was naked, but in the second it was covered with short hairs. (Text-fig. 4, B.)

One of the interests of these variations is that they break down the differences I recorded in 1910 between the feet of the Chital and of the Hog Deer (*A. porcinus*), in which the interungual tie is hairy and the glandular pouch provided with long projecting hairs. On the strength of these differences I separated *porcinus* from *axis*, retaining for it the subgeneric name *Hyelaphus*; and this opinion was adopted by Lyddeker. Owing to the identity in the structure of the hind foot in the two species,

Text-figure 4.



A. Longitudinal section of the fore foot of *Axis axis*.
B. The same of the hind foot.

Hyelaphus now falls as a synonym of *Axis* and the latter will contain two species *A. axis* and *A. porcinus*, the genus *Axis* being distinguished from the supposedly allied form *Rusa*, which has similar simple antlers, by the presence of the glandular pouch on the hind foot.

In the two examples of *A. axis* above referred to, the creamy or waxy secretion sticking together the hairs of the glandular pouch smelt like tallow candles, with an admixture of cheese. The fore feet differed in no important respect from those of the specimen described in 1910. (Text-fig. 4, A.)

In a foetal *Axis* Deer, measuring sixteen inches (about 400 mm.) from the snout to the root of the tail and weighing 3 lb., the skin although naked showed faintly all the spots characteristic of the adult. The tail was relatively much longer than in the adult.

The eyes were closed. The only hairs developed were the sensory vibrissæ on the head, the mystacials, submentals, superciliaries, and suboculars being very evident. On the cheek there were two genals and the interramals arose from a warty excrescence. The early development of all the tufts of vibrissæ characteristic of the Mammalia is interesting. The position of the antlers was marked by a depression of the integument on each side of the crown of the head. The preorbital gland was represented by a shallow depression, opening by a short linear orifice a little distance below and in front of the eye. The metatarsal gland was marked by a small pale oval patch on the skin of the leg below the hock. The pedal glands were as in the adult, a deep pit on the hind foot and a shallow pit on the fore foot.

Genus DAMA Frisch.

DAMA DAMA Linn. (p. 950).

The rhinarium in the Fallow-Deer is much reduced by the encroachment of hair from the muzzle and lips. On its upper-side the hair extends nearly as far as the anterior end of the nostrils, leaving only a narrow strip bordering the nostrils laterally above. The infranarial portion is very narrow inferiorly, being at its narrowest point much less than the width of the space between the nostrils. (Text-fig. 3, B, C.)

Genus ELAPHURUS M.-Edw.

ELAPHURUS DAVIDIANUS M.-Edw. (p. 945).

My notes upon this species in 1910 were based upon the observations of others and upon the examination of a dried skin in the British Museum. Since then I have seen two examples in the flesh, both from the Duke of Bedford's herd at Woburn. The first of these, a male, died in the Zoological Gardens from impaction of the psalterium in August 1917; the second, a female, died at Woburn and was kindly sent to me for examination by the Duke in January 1923.

The *facial vibrissæ* are represented by well-developed buccal and orbital bristles; by a small genal tuft on each side below the corner of the eye and above the line of the mouth, and by an interramal tuft of a few short bristles arising from a small elevation. In the male there is an interramal dew-lap which is absent in the female. Perhaps this is seasonally developed.

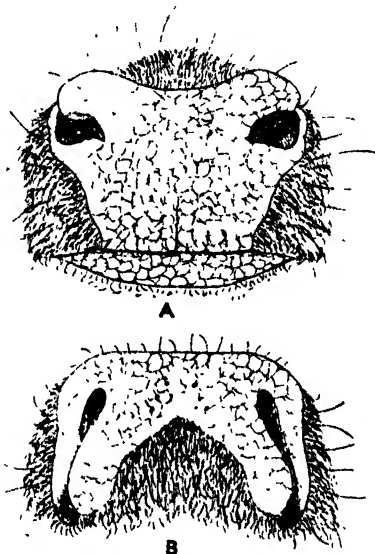
The *rhinarium* is large and naked with the nostrils narrow and widely separated, but with the space between them a little narrower than the infranarial portion, which has a short inferior median sulcus. On the upperside the hair of the muzzle encroaches to a great extent between the nostrils, reaching beyond

the middle of their length, but leaving a wide naked rim above them laterally. Although the rhinarium differs considerably in its nakedness from that of *Cervus canadensis* or *Dama dama*, it is not very unlike that of *Cervus eldi*. (Text-fig. 5, A, B.)

The *preorbital gland* is a deep and long pit, with a naked floor, its orifice when closed being about as long as the eye.

The *ear* is moderately large and thickly clothed with long hairs inside. It has three vertical ridges, the anterior and posterior being stronger than the median. The basal ridge is bilobed, the posterior lobe is much longer than the anterior, but not very much higher, and has a convex edge. Beneath it there

Text-figure 5.



A. Rhinarium and edge of lower lip of *Elaphurus davidianus*, from the front.

B. Rhinarium of the same from above.

is a curved rounded ridge leading down to the orifice. (Text-fig. 15, A.)

The *feet* are long and broad with the digits widely separable, owing to the shallowness of the interdigital web arising from the depth of the depression between the heels of the hoofs. The upper interdigital depression is approximately as deep as in *Cervus elaphus* or *maral*, and is scantily covered with hairs in its proximal half, naked in the distal half. The hoofs themselves are moderately wide and pointed, but are remarkable for the exceeding length of the heels, which extend backwards almost to

the false hoofs—the latter being exceptionally long, particularly on the fore feet. The area between the false hoofs is naked, except for a narrow strip of hair running on each side from the back of the leg to the heel. The deep depression between the heels is entirely naked. The hind feet differ from the fore feet in being smaller and in having relatively shorter false hoofs. The feet of the female in the winter were more hairy below than those of the male in summer described, above. The wide separation of the digits and the length of the heels and of the false hoofs suggest adaptation to swamp-life. (Text-fig. 6, A, B.)

The *metatarsal gland* may, it appears, be present or absent. It is present on the skin in the British Museum; but I could find no trace of it in the female, and have no note on the subject in the male.

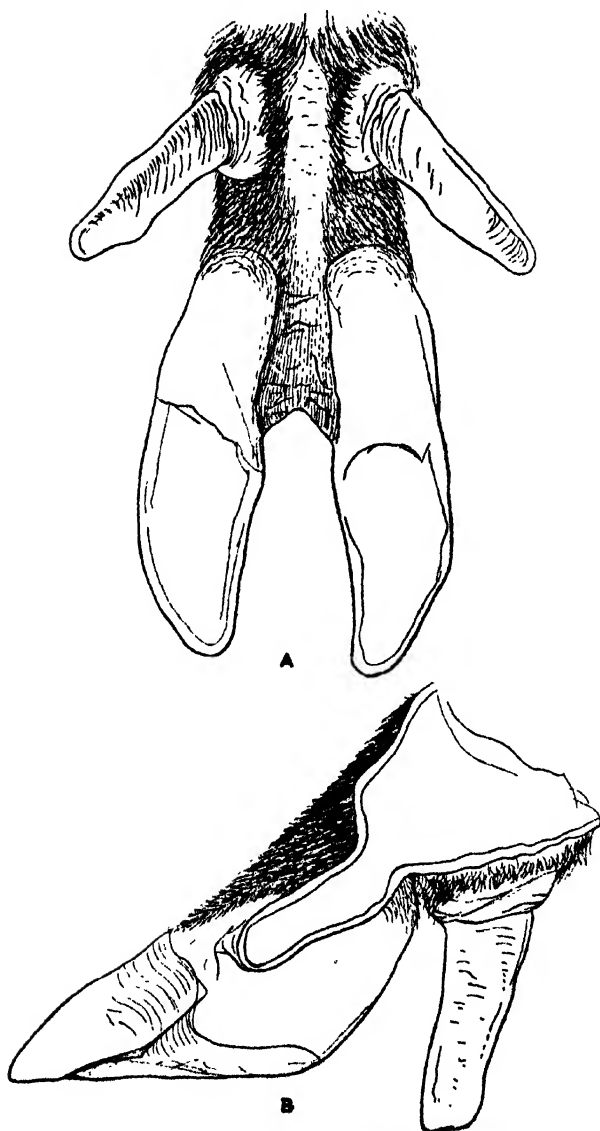
The *penis* is truncated apically and provided with five pairs of lobes which normally fold over the urogenital orifice, but are capable of spreading out like the petals of a flower. Except, however, that the lobes are somewhat better defined, the penis does not differ essentially from that of *Cervus xanthopygus* and of other typical deer of the Old World. (Text-fig. 17, E, F, G.)

It may be recalled that, according to Garrod (P. Z. S. 1877, p. 9), the penis of the American deer now referred to the genera *Odocoileus*, *Mazama*, *Pudu*, and others differs from that of such Old World deer as *Cervus*, *Axis*, *Dama*, etc., in being attenuated at the apex, the urethral canal being produced into a median slender process, unlike the upcurled termination of the urethra, which does not project beyond the truncated tip of the glans in the Old World forms. Hence the discovery of the structure of the penis in *Elaphurus* is the final piece of evidence required to establish the affinity of that genus with the typical Old World deer and to sever it from the American genera with which Lydeker affiliated it.

*Notes on the Seasonal Colour-change and Antler-growth of
Elaphurus.*

Even as recently as 1915, the colour of *Elaphurus* was described as "reddish tawny with a tinge of grey" by Lydeker, who judged apparently from the mounted specimen in the British Museum, which was presented to that institution by the Duke of Bedford in July 1899. As a matter of fact, the reddish tint is a transient phase lasting some three or four months of the summer season, roughly from May or June to August or September. For the remaining eight or nine months of the year the animal is the colour of a grey donkey; and this grey coat is thick and luxuriant in the winter, whereas the reddish coat is comparatively short and sparse.

Text-figure 6.



A. Lower side of fore foot of *Elaphurus davidianus*.
B. Section of fore foot of the same.

The stag presented to the Society on January 26th, 1916, by the Duke of Bedford was in the grey pelage. This was replaced by the red pelage in June, and the grey phase was assumed in September and carried through the winter until May 1917, when the red summer coat was substituted. The first clear signs of the shedding of this red coat were noticed on July 23rd. It came away with great rapidity and was all gone in about a week's time, except on the crown of the head, where it persisted until the stag's death in August.

The red phase was therefore about a month earlier in its appearance and disappearance in 1917 than in the previous year.

With regard to the antlers, the stag was carrying a burnished pair on its arrival on January 26th, 1916. These were shed on February 1st. The new antlers grew rapidly and were burnished by the time the grey pelage was replaced by the red pelage in midsummer, when rutting set in. These antlers were shed on October 22nd, and a new pair started at once; but instead of reaching their full size in the winter and being shed in February as in the previous year, they continued to grow through the winter and spring, began to peel in May, coincidently with the shedding of the grey winter pelage and the appearance of the red summer coat, and were unshed at the time of the stag's death in August. Being the result of about seven months' growth, these antlers were much larger than the preceding pair, which were developed in about four and a half months.

But, as recorded by Lord Tavistock in a letter to me, the antler-shedding in *Elaphurus* is a much more complicated and variable phenomenon than those who have seen single stags are aware. The following is the substance of his observations made upon the herd at Woburn:—

No immature stag grows more than one pair of antlers in a year. The antlers of a yearling are not clean till the end of June and are shed in midwinter or even later. The antlers of a four-year old stag are shed early in November, and may not be clean for three weeks after those of the old stags have lost their velvet. All old stags clean and shed their summer antlers with as little variation as to date as red deer. But the date of the cleaning and shedding of their winter antlers is exceedingly variable. In the case of late shedding of the winter antlers, stags will sometimes be found in May with but very few inches of new velvet-covered antlers; but, no matter how small the growth, these antlers will harden and clean in time for the rutting season. These stumpy-horned stags, however, have very poor chance against their better-armed companions, and it is only when the latter are exhausted at the end of the season that the former have any chance of collecting a harem at all.

Very large antlers of *Elaphurus* are always the result of a winter growth by an adult animal; but the production of a

single pair of antlers of large size instead of two pairs of small or medium size becomes increasingly rare the longer the deer remain in this country. The result is now that the only really handsome heads are those carried by stags five and six years old. As a rule, there is no attempt to resume the rut when the winter antlers harden, the stag remaining as lazy and peaceful as if still in velvet; but one or two stags were known to Lord Tavistock which for several seasons recommenced calling in midwinter. November was the latest month in which he heard stags, still carrying their summer horns, calling; and he has seen a six-year old stag, in full summer coat and carrying a large pair of horns, herding his hinds with great energy and calling in the first week in February. The antlers in this case were the continuous growth of the whole autumn and winter.

The majority of the calves are born in April and May. Very late ones are not common.

In 1922 Ludwig Zukowsky, Hagenbeck's assistant, published a paper* upon *Elaphurus davidianus*, based upon a specimen that was exhibited for nearly two years at Stellingen. Unfortunately, the author was not acquainted with the published literature on this subject. He described in detail the mode of growth of the antlers, and quite correctly spoke of the anterior branch as the "brow-tine." In this he confirmed in every particular my account published in 1912 (P. Z. S. pp. 777-780) from sketches kindly supplied by Lord Tavistock, the accuracy of which I was subsequently able to verify on the specimen exhibited in the Zoological Gardens†. Zukowsky also recorded the succession of the antlers in this aberrant species. The specimen at Stellingen cast its antlers on the following dates: March 8, 1913, Sept. 18, 1913, March 17, 1914, Oct. 5, 1914, and died on Dec. 30, 1914, with fully developed antlers in velvet.

When Hagenbeck's specimen died it was sent to be mounted to the Natural History Museum, Hamburg, and Herr Gast, Superintendent of that institution, subsequently wrote to Zukowsky to inform him that he had found just beneath the edge of the under lip "a deep sheath or vagina let into the skin, which seemed to point to a glandular duct, one inch in length." I failed to find any trace of this structure in the female specimen of *Elaphurus* which the Duke of Bedford sent to me for the special purpose of investigating this gland. Possibly there may be such a gland restricted to the male; but, so far as is at present known, the cutaneous glands in the Cervidæ are alike in the two sexes‡.

* I am indebted to the Duke of Bedford for kindly sending me a copy of this paper, which was published in Arch. Naturg. vol. lxxxviii., May 1922.

† When I first suggested in 1910 that the anterior and posterior branches of the antlers of *Elaphurus* are strictly homologous with the "brow-tine" and "beam" respectively of the antlers of ordinary Cervidæ, I was not aware that I had been anticipated in this view by Dr. Theodore Gill, who came to the same conclusion. This was published I believe in 'Forest and Stream,' but I do not recollect the reference.

‡ Following Garrod, I exclude *Moschus* from this family.

Genus HYDROPOTES Swinh.

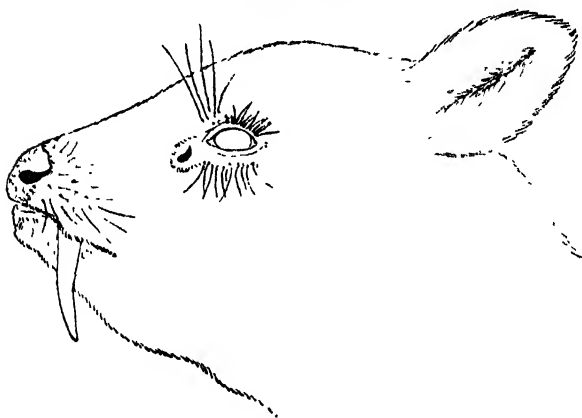
HYDROPOTES INERMIS Swinh. (p. 956).

Some of the external characters and the visceral anatomy of this aberrant genus were described by Garrod (P. Z. S. 1877, pp. 789-792). Additional information was later supplied by Forbes (P. Z. S. 1882, p. 637).

The head is remarkable for the complete absence of all trace of antlers—a feature in which this genus is unique in the Cervidæ,—the long, slightly curved, pointed and movable upper canines, and the narrow muzzle. (Text-fig. 7.)

The lightly areolated *rhinarium* has a deep wide infranarial portion, which is wider than the supranarial portion and therefore much wider than the internarial area. The latter is of normal

Text-figure 7.

Head of *Hydropotes inermis*.

width. The supranarial portion is unusually high, so that the height of the entire rhinarium, as described by Garrod, is about equal to its width. (Text-fig. 8, C.)

The mystacial *vibrissæ* are tolerably numerous and of average length. The superciliaries and infraorbitals are also normally developed; but in the thick hairs of the cheek and throat I can find no trace of genal or internarial vibrissæ, which are sometimes present but never abundant in other Cervidæ.

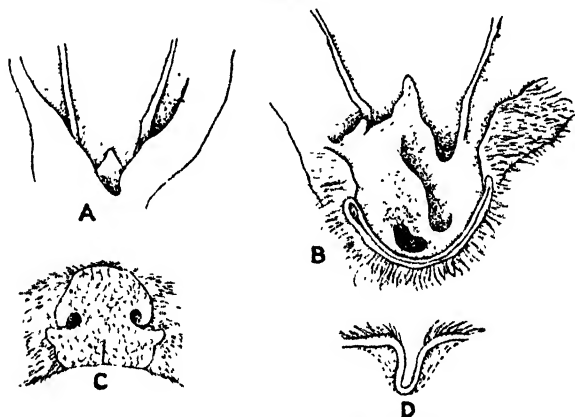
The *preorbital gland* is represented by a small shallow pouch lodged in a naked area of skin just in front of the eye. (Text-figs. 7; 8, D.)

The *ear* is short and broad, and densely clothed within with hairs, which meet in the middle line of the hollow of the pinna.

The overfolded edges of the base of the ear meet at an acute angle. There are two vertical cartilaginous ridges, an anterior and a posterior, supporting the pinna; and the prominences on the basal ridge are very unequal in size, the anterior being quite small and slender, whereas the posterior rises as a high triangular peak. These prominences are quite unlike those of any other species of Cervidæ that I have examined. (Text-fig. 8, A, B.)

Feet.—The hoofs of the fore foot are long and pointed, and tolerably widely separable; the soft inferior cushion, constituting the greater part of the sole, is continued backwards some distance behind the smooth heel-tie which joins the heels together. On the front of the pastern there is a tolerably deep and smooth

Text-figure 8.



- A. Base of ear of *Hydropotes inermis*.
- B. The same cut open.
- C. Rhinarium of the same from the front.
- D. Section of preorbital gland of the same.

glandular depression, and the skin all along the back of the pastern from the heel-tie to the area between and beyond the false hoofs is also glandular. This area is more scantily covered with hair than the area of the leg above the false hoofs, and the false hoofs themselves, which are short, are basally encircled by an area of naked skin divided inferiorly by a narrow scantily hairy strip of skin. (Text-figs. 9, A; 10, A.)

The hind foot is very similar to the front foot, but the hoofs are rather more widely separable, and the heels are narrower and a little longer. As in the front foot the back of the pastern is hairy down to the heels, and the heel-tie is naked. The glandular depression is considerably deeper and longer, and has a more abruptly upturned anterior rim. The widely separable

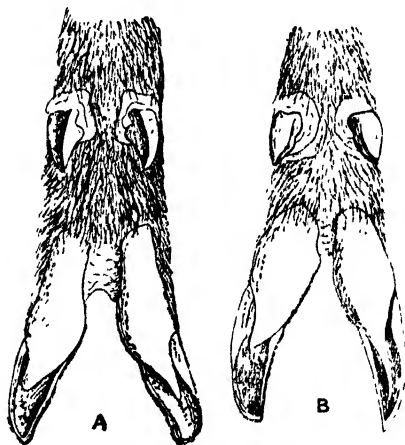
hoofs with their long heels are adapted for progression upon soft marshy ground. (Text-figs. 9, B; 10, B.)

There is no trace of metatarsal or tarsal gland.

The *anus* opens in the upper half of an oval naked area of skin, broader above than below and extending from the root of the tail nearly to the scrotum. The orifice is surrounded by a thickened glandular rim. The edge of the smooth oval area is sharply defined by the thick growth of hair, which is as luxuriant here as elsewhere on the body. The tail is short, only long enough to cover, when depressed, the smooth anal area, and is thickly covered with hair below as well as laterally and above. (Text-fig. 11, B.)

The *inguinal region* has a single pair of teats—not two pairs as recorded by Garrod in the newly-born fawn. The area between them is scantily clothed with long hairs; but on the outer

Text-figure 9.



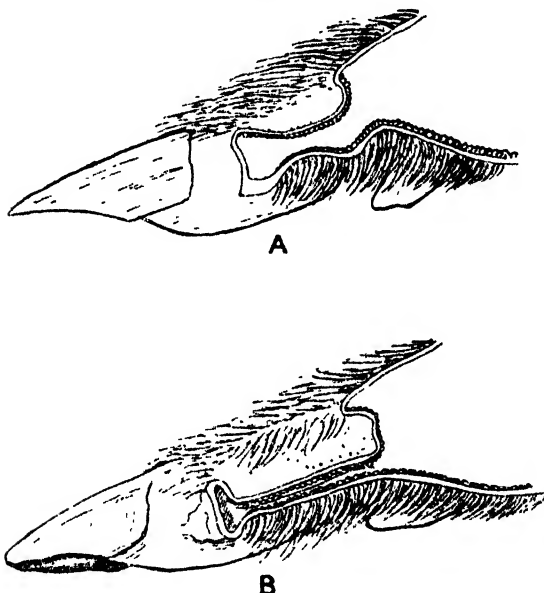
A. Lower side of fore foot of *Hydropotes inermis*.
B. The same of the hind foot.

side of each there is a large nearly naked area of skin extending a considerable distance outwards and backwards; and towards the outer edge of this there is a shallow, curved, glandular depression, recalling the inguinal glands of many of the Bovidæ. This is the first record of the presence of inguinal glands in the Cervidæ. (Text-fig. 11, A.)

The *prepuce* is a naked button of skin surrounded by long hairs and occupying the normal abdominal position in front of the inguinal region and remote from the scrotum. The *penis* is perfectly simple, straight, and slightly attenuated, with the orifice terminal. It runs between a couple of ridges in the dorsal wall of its sheath. (Text-fig. 11, A.)

The absence of antlers and the presence of large upper canine teeth in *Hydropotes* naturally suggested the possibility of kinship between it and *Moschus*. Since Garrod definitely disposed of this view, it need not be further discussed. He closed his account of the anatomy of *Hydropotes* as follows:—"To what group of the Cervidæ *Hydropotes* is most allied there is still considerable uncertainty. That it is not allied to the New-World type is evident from its vomer not extending downwards to join the osseous palate posteriorly. That it is not Cervuline [related to the Muntjacs, which also have large canines] is equally certain on

Text-figure 10.

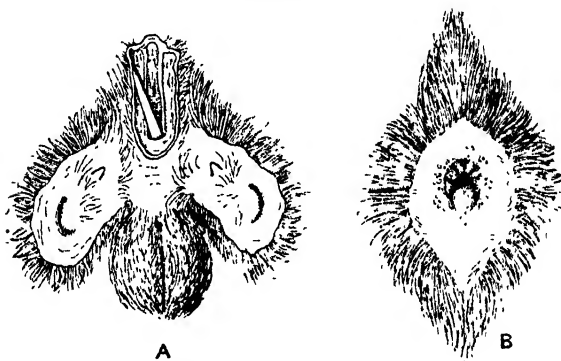
A. Section of fore foot of *Hydropotes inermis*.

B. The same of the hind foot.

account of its cuneiform bones being free from the naviculo-cuboids. Its large Spigelian lobe favours the view suggested by Sir Victor Brooke, that it is most closely allied to the Rusine Deer" (p. 792). This view, I think, may be dismissed without hesitation. On the other hand, Forbes's opinion (P. Z. S. 1882, p. 637) that *Hydropotes* is related to *Capreolus* is worth more consideration. The two, at all events, agree in being "telemetacarpalian" and in the structure of the vomer and apparently of the glans penis. But the differences between them are too many and too deep-seated to admit of close affiliation. In the first place, *Hydropotes* is the most primitive of all existing Cervidæ in

the complete absence of the antlers and the presence of long tusk-like canines in the male. *Capreolus*, on the other hand, has well-developed branched antlers, and has normally lost all trace of the canine, being in the latter particular more specialised than *Cervus*. Again, *Capreolus* has lost the preorbital and retained the metatarsal gland. *Hydropotes* has retained the preorbital and lost the metatarsal gland; and has acquired inguinal glands, a new feature in the Cervidæ. The differences between the two in the length and separability of the hoofs are also marked; but, considering the differences of habitat, they are not obviously an indication of remoteness in kinship. The deep and long interdigital glandular depressions in *Hydropotes*, on the contrary, are

Text-figure 11.



- A. Inguinal and genital area of *Hydropotes inermis* ♂, showing the nearly naked area of skin on each side, with a single pair of testis and the shallow pouches of the inguinal glands. The sheath of the glans penis cut open along the middle line, showing the glans turned towards the right and the two ridges forming the groove along which it runs.
- B. Anal area of the same with the tail raised, showing the anus insunk in the surrounding glandular area.

much more primitive than the pouch-like gland of the hind foot of *Cervulus*.

In view of the peculiarities of *Hydropotes*, I propose to separate the genus from the rest of the Cervidæ as the type of a special subfamily, Hydropotinae.

Genus *ODOCOILEUS* (= *Dorcelaphus*).

ODOCOILEUS VIRGINIANUS Bodd. (p. 962).

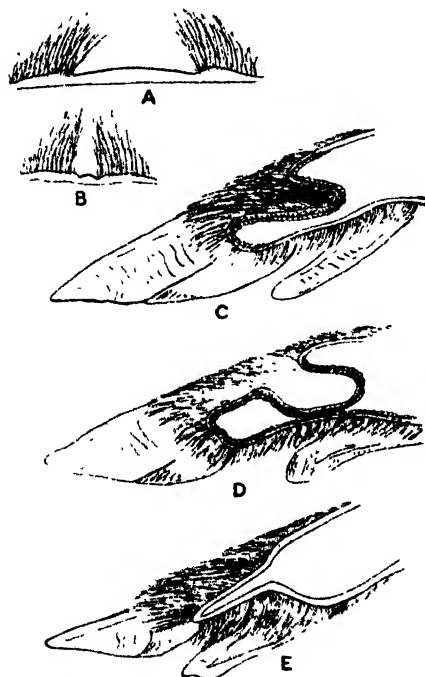
In 1910 I had seen no fresh example of this species, quoted as *Dorcelaphus americanus*, and was only able to describe the glands in the feet, as shown by specimens in the Museum of the College

of Surgeons. Since then I have examined an adult female that died in the Gardens on August 28th, 1911.

The *rhinarium* is large and naked, the hairs of the muzzle encroaching but little on its upper surface; the infranarial portion is wider than the space between the nostrils.

The *preorbital gland* is represented by a very small, shallow pit.

Text-figure 12.



- A. Longitudinal section of the metatarsal gland of *Odocoileus virginianus* (typical form).
- B. Transverse section of the same.
- C. Section of fore foot of *O. virginianus spinosus*.
- D. Section of hind foot of the same.
- E. Section of fore foot of *Moschus moschiferus*.

The *tarsal gland* consists of a patch of thickened vascular skin covered by a thick pad of long hair stuck together with secretion, but without any under-fur; the hairs are umber-brown with white bases.

The metatarsal gland shows externally as an elongated patch of naked, horny, granular skin overlapped by the long, mostly

white hairs growing round it. The secreting glands lie beneath these long hairs, the skin being thicker and more vascular there than elsewhere. The naked area between the long hairs seems to serve as a receptacle for the secretion, since it collects and is encrusted there. (Text-fig. 12, A, B.)

The feet and pedal glands are as described in 1910, except that the pouch on the hind foot is rather more capacious, has a wider orifice and naked walls. The pouch on the fore foot is similar, but only about half the size.

ODOCOILEUS VIRGINIANUS SPINOSUS Gay & Gervais (p. 962).

In 1910 I referred to a living example, identified as *Dorc-elaphus americanus savannarum*, which came from Venezuela and was presented to the Society by Major Albert Pam. The animal died in 1914, and I was able to examine it in a fresh state.

The rhinarium resembles very closely that of the typical North-American form, but from my sketches it seems that the infranarial portion is somewhat narrower inferiorly and the upper surface a little more overgrown with hair in the middle. (Text-fig. 14, A.)

The vibrissæ on the upper and lower lips and above and below the eye are well developed; but there is a single long genal bristle arising beneath the posterior angle of the eye and far back in a line with the mouth. There is no interramal tuft.

The preorbital gland is small as in the typical form.

The tarsal gland is marked by a thickened bunch of hair, brown and white in colour, and covered at the base with secretion.

The metatarsal gland is a very small patch of thickened skin overgrown with white hair.

The glands are well-developed pouches, both on the front and the hind foot. The hind foot hardly differs at all from that of the typical *O. americanus*, the walls of the pouch being naked; but in the fore foot the walls of the pouch are thickly covered with hair and the orifice is much longer than in the typical *O. virginianus*, with the heel-tie shallower. There is also a small naked patch at the posterior inferior angle of the heel-tie. (Text-fig. 12, C, D.)

In this animal, as in the above-described example of the typical *O. virginianus*, the false hoofs of the fore foot are much longer than those of the hind foot.

ODOCOILEUS VIRGINIANUS PERUVIANUS Gray.

A male example from Iquique, presented by Miss Peggy Lomax on April 24 in 1911, died in Jan. 1923 from pneumonia, the worn condition of the teeth showing it to be an old animal. The donor informed me that it was born in 1909. It was therefore

in its fourteenth year. This was the unidentified specimen of *Odocoileus*, of which I described the antler-growth in 1912 (Proc. Zool. Soc. pp. 781-783) to indicate the homology between the so-called "subbasal snag" of the genus *Odocoileus* and the "brow-tine" of *Cervus*.

The description given above of the external characters of *O. v. spinosus* applies very closely to this form. The only variations noted were the presence in *O. v. peruvianus* of a pair of long interramal vibrissæ, of longish hairs on the sides of the glandular pouch of the hind foot, and the reduction in the size of the metatarsal gland. This gland was merely represented superficially by an inconspicuous patch of hairs slightly longer and slightly different in tint from those of the surrounding area of the lower half of the metatarsal area. The skin beneath this felt slightly thicker to the touch, but the only indication of secretion was a small scab on the gland of the right side. This gland was not visible to me in the living animal, and I thought it was absent. It might very easily be overlooked in prepared skins; and this would account for *O. v. peruvianus* having been described as without metatarsal glands. Not improbably they may be sometimes altogether aborted in this subspecies.

The *tarsal gland*, on the contrary, is represented by a large thick mat of longish hairs, which, upon being separated, showed as a mixture of grey and black with yellow secretion at the base.

The *ear* is tolerably large and nearly naked, as in the related race *O. v. gymnotis*. It has two vertical cartilaginous ridges, of which the posterior is much the stronger. Inferiorly it forms the posterior border of a deepish pit, the anterior border of which is a rounded ridge descending from the rounded posterior lobe of the basal ridge. The anterior lobe of this is a little smaller than the posterior; there is a low short longitudinal crest on its outer side, and the anterior vertical ridge terminates on its inner side. A thickened rounded crest, defined in front and behind by a hollow, descends to the bottom of the cavity of the ear and the orifice opens in the anterior hollow. (Text-fig. 15, B.)

The *penis*, as pointed out by Caton for the North-American forms of *Odocoileus*, was pendulous from a point just in front of the scrotum. The tip of the prepuce was almost naked, but just within its orifice were some hairs arising from definite papillæ. The glans, as in other American deer examined, agrees exactly with Garrod's description, ending in a narrowed point with terminal orifice. (Text-fig. 17, A, B.)

Within the limits of the genus *Odocoileus* the preorbital gland and the pedal glands appear to be always present, the latter occurring on both hind and front feet. According to Caton, they are, however, relatively smaller in *O. hemionus* than in *O. virginianus*, *O. columbianus* coming between the two in this particular.

The metatarsal and tarsal glands are variable. The former attains its maximum in development in *O. hemionus*, where, according to Caton, the bare patch of skin overlapped by long hairs may be five or six inches long. In North American examples of *O. virginianus* it varies from less than one inch to an inch and a half in length, whereas in some of the southern forms (such as *O. v. toltecus*, *acapulcensis*, etc.) it is absent. The tarsal gland varies in size and colour according to the species; but I do not know whether it is absent or not. According to Caton, its hairs expand under excitement, like the hairs of the tail and rump, in the North American species.

Genus *MAZAMA* Raf. (p. 962).

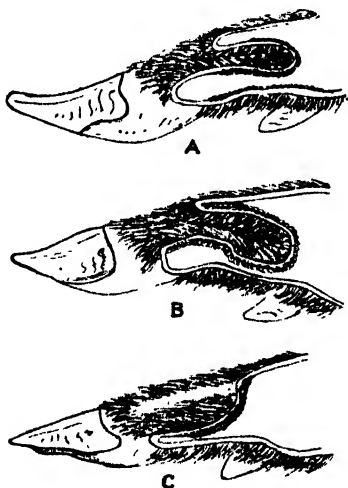
The two species of this genus previously described were *M. nemorivagus* (p. 962) and *M. bricenii* (p. 964).

MAZAMA TEMA Raf.

A single male example from Guatemala, which died on April 26th, 1914.

The *rhinarium* is naked above almost as far back as the

Text-figure 13.



- A. Longitudinal section of the fore foot of *Mazama tema*.
- B. The same of the hind foot.
- C. The same of the hind foot of *Pudu pudu*.

posterior angles of the nostrils and the infranarial portion is very wide, showing laterally as far back as the middle of the nostrils, as in *M. nemorivagus*. (Text-fig. 14, C.)

The normal labial and ocular *vibrissæ* are present; the genal tuft is represented by two bristles beneath the posterior corner of the eye and as low as the line of the mouth; the interrimal tuft is composed of three bristles a little behind a line joining the corners of the mouth.

The *preorbital gland* is a small shallow depression, as in *M. nemorivagus* and *M. bricenii*.

The *tarsal gland* is represented by a small tuft of hair, as in *M. nemorivagus*.

The *metatarsal gland* is absent as in *M. nemorivagus* and *M. bricenii*.

The *pedal glands* on the fore foot are much larger and deeper than in *M. nemorivagus* and *M. bricenii*, resembling those of *O. virginianus spinosus* in depth, but having a shorter orifice. The walls are thickly hairy. The heel-tie also is lower than in the other species of *Mazama* and is altogether naked, and the heels of the feet are long and the hoof moderately so. (Text-fig. 13, A.)

The pouch on the hind foot is larger than on the fore foot and has thickly hairy walls as in *M. bricenii*. In this foot also the heel-tie is naked, the heel is long, but the hoof is short. (Text-fig. 13, B.)

This species differs from the other two species of *Mazama* in the large size of the gland of the fore foot. The nakedness of the heel-ties on both fore and hind feet is a character unrecorded elsewhere in the Telemetacarpalian deer.

Genus PUDU Gray.

PUDU PUDU Mol. (p. 967).

The head of this species is remarkable for the forward growth of the hair from between the ears to the summit of the crown, where it meets and forms a crest with the backwardly growing hair of the muzzle and forehead.

The *rhinarium* is tolerably large and lightly areolated; the supranarial portion is mostly naked above, the hair only encroaching upon it to a slight extent posteriorly; the infranarial portion is mesially grooved; it is narrower than the supranarial portion, but a little wider than the space between the tolerably widely separated nostrils. (Text-fig. 14, B.)

The *facial vibrissæ* are represented by some shorter mystacial and submental and longer superciliary and subocular bristles, there being no trace of genal or interrimal tufts.

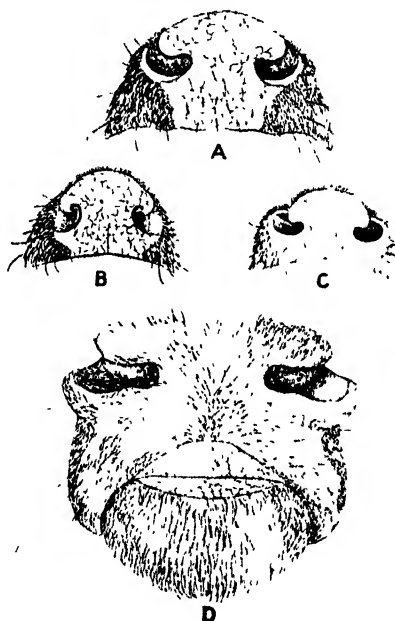
The *preorbital gland* is a comparatively small and shallow pouch, opening on a naked area a little in front of the eye.

The *ears* are rounded, the expanded portion being supported by

four vertical ridges; the basal internal ridge has an angular prominence, which is as high as its posterior rounded termination. (Text-fig. 16, D.)

The *feet* have pointed hoofs with a tolerably short heel and short false hoofs. On the hind foot there is a deep and long interdigital glandular depression, the integument of its floor being almost in contact with that of the back of the pastern. The distal or anterior edge of this depression is not elevated, the heel-tie being shallow and smooth. The walls of the depression

Text-figure 14.



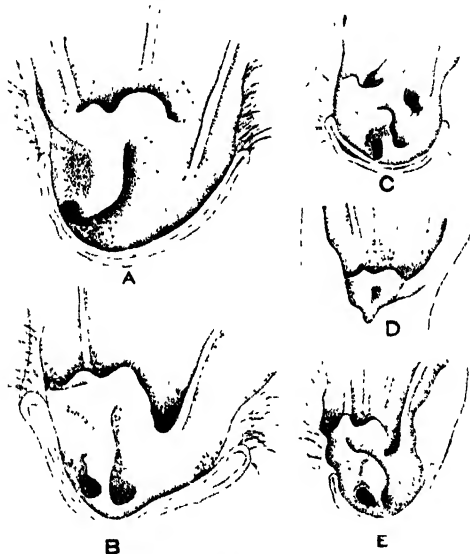
- A. Rhinarium of *Odocoileus virginianus spinosus*, from the front.
- B. The same of *Pudu pudu*.
- C. The same of *Mazama temia*.
- D. The same of *Rangifer tarandus*.

are clothed with hair, which is rusty yellow towards the mouth and white near the bottom. The depression on the fore foot is very similar, but a little shallower. Both tarsal and metatarsal glands are absent. (Text-fig. 13, C.)

In the brief description given by Flower (P. Z. S. 1875, p. 160) of the feet of this species it is said that the pedal glands are not represented by distinct pouches, "but the skin in the depression between the toes . . . is bare and evidently has a free sebaceous

secretion, representing, in the author's opinion, the most rudimentary or earliest stage of an interdigital gland." How little this account accords with the actual facts may be seen by comparing it with the description given above. I was completely misled by Flower into imagining that the interdigital areas in the Pudu resemble those of *Cervus*, surprising as such a conclusion was. There is in reality no such resemblance. The depressions are like those of the hind foot of the Fallow-Deer (*Dama dama*) and of the Muntjacs (*Muntiacus = Cervulus*) and *Elaphodus*, which I described and figured in 1910: that is to say, they

Text-figure 15.



- A. Base of ear of *Elaphurus davidianus*, cut open.
- B. The same of *Odocoileus virginianus peruvianus*.
- C. The same of *Tragulus*.
- D. The same of *Pudu pudu*.
- E. The same of *Muntiacus muntjak*.

belong to what I believe to be the most primitive type of pedal gland in the Cervidæ—a long deep depression the floor of which is in contact, or nearly so, with the integument of the back of the pastern. No other genus of Cervidæ inhabiting America has feet of this type, so far as is known. *Cervus canadensis* may be set aside as an alien from Asia; but in *Rangifer*, *Odocoileus*, and *Mazama* the glandular depression of the hind foot is a deep pouch with constricted orifice, whereas in the front foot it is a small shallow pit, the heel-tie in both cases being deep.

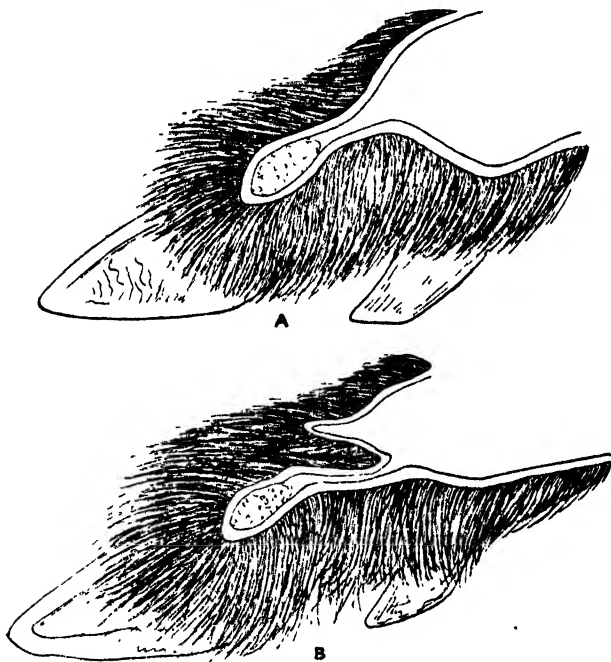
Genus RANGIFER H. Smith.

RANGIFER TARANDUS Linn. (p. 960).

In 1910 I was only able to examine the dried limbs of the North American race of this species, *R. tarandus caribou*. That account I can now supplement by observations upon a female specimen that died in the Gardens on July 27th.

The muzzle of the Reindeer has been described as covered with hair, as if there was no trace of rhinarium. It is true that the

Text-figure 16.

A. Section of fore foot of *Rangifer tarandus*.

B. The same of hind foot.

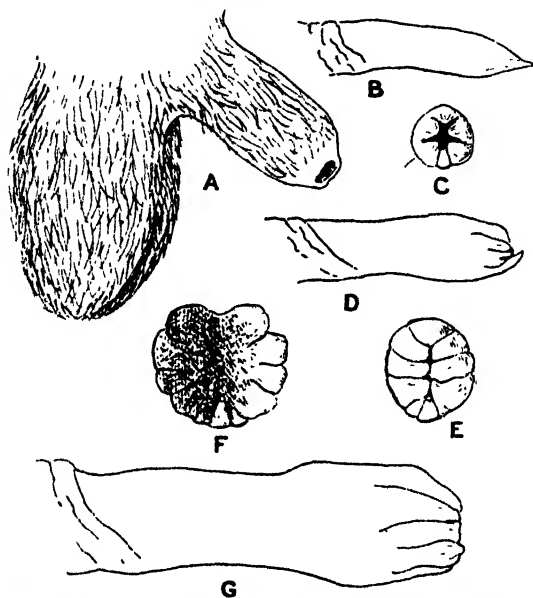
area above, between, and below the fleshy valvular nostrils is entirely overgrown with short soft hair; but along the edge of the upper lip there is a naked areolated tract, wider than the space between the nostrils, with convex upper edge and similar in sculpture and width to the corresponding tract on the edge of the lower lip, but about twice as deep. (Text-fig. 14, D.)

This is the inferior portion of the rhinarium retained. In this particular the Reindeer is unique amongst the Cervidæ.

The external appearance of the well-developed tarsal gland was fully described by Caton, and I have nothing to add to his description or to my account of it published in 1910. The metatarsal gland, as Caton and others have stated, is absent.

My first account of the feet, taken from dried specimens, requires some modification. On the fore foot of the fresh specimen there is a deeper depression on the front of the pastern; and on the

Text-figure 17.



- A. Penis and scrotum of *Odocoileus virginianus peruvianus*, showing the long pendulous prepuce close to the scrotum.
- B. Glans penis of the same.
- C. Apex of glans penis of *Cervus (Sika) hortulorum*, from the front.
- D. Glans penis of the same from the side.
- E. Apex of glans penis of *Elaphurus davidianus*, with lobes folded, from the front.
- F. The same with lobes expanded.
- G. Glans penis of the same from the side.

back of the pastern the depression is deeper still, the integument forming the floor of the posterior depression being almost in contact with that of the anterior depression, so that the two digits are joined together by a very shallow fold or loop of integument. This loop expands towards the hoofs, and the expanded portion is filled with a mass of soft, fatty, somewhat gelatinous material. But there is no trace of a glandular pouch

on the fore foot *. It is to the remarkable shallowness of the integumental fold between the digits and the depth of the depression on the back of the pastern that the wide separability of the hoofs in *Rangifer* is due. The skin of the interdigital depressions is everywhere covered with long thick hair. In the hind foot, the posterior depression of the pastern is not so deep as on the fore foot, but the integumental fold is very similar, although even shallower proximally. On the front of the pastern the depression is deeper and forms a deep glandular pocket very like that of *Odocoileus*. (Text-fig. 16, A, B.)

A species which even surpasses *Rangifer* in the extreme shallowness of the heel-tie and the depth of the depressions between the digits is the Musk-Deer (*Moschus*), which has the hoofs similarly separable for progression on soft snow and for the sure-footed descent of steep slopes. (Text-fig. 12. E.)

Classification of the Cervidæ.

In 1910 I divided the Cervidæ into two subfamilies, Capreolinae and Cervinae, corresponding respectively to Sir Victor Brooke's divisions Telemetacarpalia and Plesiometacarpalia. It appears to me that we must adopt Brooke's primary grouping of the family; but that the genera of both groups, more particularly of the Telemetacarpalia, are too diversified to be assigned to the two subfamilies proposed. It may be chained at all events. I think, that the subfamilies tabulated below are as well defined as the subfamilies of the Bovidæ:—

- | | |
|---|----------------------|
| a. Distal ends of lateral metacarpals retained, proximal end aborted (Telemetacarpalia). | |
| b. Vomer dividing the posterior nares. | |
| c. Naviculo-cuboid and external cuneiform bones of tarsus united; pedal glands a deep long cleft, with shallow heel-tie | <i>Pudinae.</i> |
| c'. Naviculo-cuboid and external cuneiform bones separated; feet with pouch-like pedal glands and deep heel-tie. | |
| d. Antlers present in males only; prepuce long, scrotal in position; feet compact, tightly tied at the heels; rhinarium large and normal | <i>Odocoileinae.</i> |
| d'. Antlers in both sexes; prepuce short, abdominal; feet widely separated at the heels; only the labial portion of the rhinarium retained | <i>Rangiferinae.</i> |
| U. Vomer not dividing the posterior nares. | |
| e. Antlers absent, male with large upper canine tusks; inguinal glands present; tarsal and metatarsal glands absent; pedal glands deep long clefts | <i>Hydropotinae.</i> |
| e'. Antlers present in males; upper canine teeth absent or minute; no inguinal glands; tarsal or metatarsal glands present; pedal glands a deeper shallow pouch on hind foot. | |

* Caton put on record the very interesting fact that in reindeer calves there are traces of a glandular pouch on the fore foot. This suggests that the pedal glands in *Rangifer* were originally present on both fore and hind feet, as they are in *Odocoileus*.

- f. Muzzle short, not swollen; rhinarium large and normal; preorbital and tarsal glands absent, etc. *Capreolinæ*.
 f'. Muzzle very long and much swollen; rhinarium reduced to a small triangular patch between the anterior ends of the nostrils; preorbital and tarsal glands present, etc. . . *Alcinæ*.
 a'. Distal ends of lateral metacarpals lost, their proximal ends usually retained, rarely vestigial or absent (*Plesiometacarpalia*).
 g. Naviculo-cuboid and external and median cuneiform bones of the tarsus fused into a single bone. Large upper canine tusks present in males; antlers supported on a long hairy pedicel . . *Muntiacinæ*
 g'. Naviculo-cuboid and cuneiform bones separated. Upper canines small or absent; antlers supported on a short pedicel. *Cervinæ*.

Many of the subfamilies mentioned above—namely, Rangiferinæ, Hydropotinæ, Capreolinæ, and Alcinæ—are monotypical.

The Pudinæ contains the two genera *Pudu* and *Pudella*, the latter differing from the former in the loss of the preorbital gland and the lacrymal pits, and in having the first lower incisor much larger than the second.

To the Odocoileinæ I refer, in addition to the typical genus, *Mazama*, *Hippocamelus*, and *Blastocerus*, although the inguinal position of the prepuce and the structure of the feet are unknown in these three. If one or more of them prove to have the prepuce abdominal, I should separate such forms as a distinct subfamily on that character alone.

The Muntiacinæ* contain three genera—*Muntiacus* (= *Cervulus*), *Procops* †, nov., and *Elaphodus*. The type of the new genus *Procops* is *Cervulus fæa*, Thomas & Doria, which is generically separated from *Muntiacus* by the absence of the frontal glands, a character in which it resembles *Elaphodus*.

The Cervinæ, containing most of the Old World deer, are a highly diversified group, composed of the following well-defined genera:—*Dama*, *Axis* (+ *Hyelaphus*), *Cervus*, and *Elaphurus*. But *Cervus* itself is subdivisible into several minor groups—*Irua*, *Sika*, *Rucervus*, and *Cervus* itself—which in the future will probably take full generic rank.

* Established by Garrod under the name Cervulinæ (P. Z. S. 1876, p. 757), based on *Cervulus*, which is antedated by *Muntiacus* now in general use.

† From *Prox*, a generic name applied by Ogilby to the Muntjacs.

17. The Classification of the Sciuridæ.

By R. I. Pocock, F.R.S.

[Received February 5, 1923: Read March 20, 1923.]

(Text-figures 18-29.)

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INTRODUCTION.

In the following brief review * of the more important attempts to classify the Sciuridæ, it is unnecessary to do more than quote Gray's papers, published in 1867 (Ann. Mag. Nat. Hist. (3) xx. pp. 270-286, 323-334, 415-436). The results he achieved were of no great moment from my present point of view, but he introduced a number of new sectional names which have to be borne in mind. In 1880, Trouessart (Le Naturaliste, i. pp. 290-293, 315) made a similar but more successful and useful effort, proposing several new names but ignoring those of Gray as connoting groups composed of unrelated elements. He divided *Sciurus* into seventeen subgenera, amongst which appear such well-defined forms as *Rheithrosciurus* and *Xerus*, which he regarded as equivalent to *Neosciurus*, *Parasciurus*, *Echinosciurus*, and *Tamiasciurus*, dismembered from *Sciurus* on certain comparatively trivial characters presented by some of the American species.

The most important contribution to the subject was made in 1893 by Forsyth Major (Proc. Zool. Soc. 1893, pp. 186-190) from a study of the teeth and skulls. He recognised the three subfamilies Sciurinae, Pteromyinae, and Nannosciurinae. The Sciurinae

* I have not here taken into account the numerous papers on American Sciuridæ which belong to four well-marked and universally admitted types—namely *Sciurus*, *Tamias*, *Citellus*, *Cynomys*, and *Marmota*. As compared with the true arboreal Squirrels of the Old World, the American species of *Sciurus* are singularly uniform in essential characters, although a large number of subgenera are admitted. *Citellus* has been similarly broken up into subgenera, and *Eutamias* has been dismembered from *Tamias*.

he divided into six genera:—(1) *Rheithrosciurus*; (2) *Xerus*; (3) *Sciurus*; (4) *Citellus* (*Spermophilus*)*; (5) *Marmota* (*Arctomys*); (6) *Cynomys*. Of these, *Rheithrosciurus*, *Citellus*, *Marmota*, and *Cynomys* were not subdivided; but both *Xerus* and *Sciurus* contained several subgenera.

Xerus was divided into five:—(1) *Protoxerus* for *stangeri*, *aubinnii* and other African species; (2) *Xerus* for *rutilus*, *capensis*, and *erythropus*; (3) *Atlantoxerus* for *getulus*; (4) *Paraxerus* for *cepapi*, *congius*, *isabella*, *lemniscatus*, and other African Squirrels; (5) *Funambulus* (*Eoxerus*) for *palmorum*, *tristriatus*, and other related Oriental Squirrels. To systematists the interesting point to notice in connection with Forsyth Major's conception of the genus *Xerus* is the inclusion in it of certain soft-furred arboreal species of African Squirrels (*Protoxerus* and *Funisciurus*) and of the Oriental Palm Squirrels (*Funambulus*), which were previously regarded as more nearly related to *Sciurus*.

Sciurus, according to Forsyth Major, comprised three subgenera:—(1) *Ratufa* (*Eosciurus*) for the large Oriental Squirrels *indica*, *bicolor*, etc.; (2) *Sciurus*, sensu stricto; (3) *Tamias* for the Chipmunks or Chipping Squirrels. *Ratufa* and *Tamias* were undivided; but the species of *Sciurus* were classified in four unnamed groups: (α) comprising certain African species, *annulatus*, *punctatus*, *rufobrachiatus*, and others; (β) Oriental species, *prevosti*, *caniceps*, *notatus*, *ferrugineus*, etc.; (γ) *rufularis*, *syriacus*; (δ) *carolinensis*, *castaneus*, *aberti*, and other American species.

In 1897 (Proc. Zool. Soc. 1897, p. 933) Thomas revised Major's classification in nomenclature and other points—so far as the genera *Rheithrosciurus*, *Xerus*, and *Sciurus* were concerned. Granting generic value to all Major's subgenera, with the exception of *Atlantoxerus* which remained a subgenus of *Xerus*, he assigned the Squirrels to the following eight genera:—*Rheithrosciurus*, *Protoxerus*, *Xerus*, *Funisciurus*, *Funambulus*, *Ratufa*, *Sciurus*, and *Tamias*. Under each of these generic names, apart from *Rheithrosciurus* and *Protoxerus*, one or more subordinate names appear; but it is not in all instances clear whether these were cited as connoting subgenera or merely as synonyms. In the case of *Xerus* it seems certain that *Geosciurus* and *Atlantoxerus* stood for subgenera; and probably that value was assigned to some at all events of the named divisions of *Sciurus*, such as *Callosciurus* and *Tamiasciurus*. But it is not likely that *Rukaria* and *Eosciurus* were looked upon as subgenera of *Ratufa*; and it is certain that *Palmista* was quoted merely as a synonym of *Funambulus*. Nevertheless great service was done by nailing each name so quoted to a type-species.

In 1898, De Winton (Ann. Mag. Nat. Hist. (7) ii. pp. 12–13) attempted to show that Forsyth Major's genus *Protoxerus* was heterogeneous, some of the species being *Xerus*-like and belonging

* In the case of nos. 4 and 5, I have adopted the names now in use for the genera, those employed by Forsyth Major being put in brackets.

to *Funisciurus* (= *Paraxerus* Major) and others to Major's section *a* of the genus *Sciurus*, for which Trouessart's name *Heliosciurus* was available. The interest of this paper lies in the circumstance that two authors working on the same material and using the same characters, namely skulls and teeth, came to very different conclusions. De Winton also commented on the curiosity and inconvenience of the fact that in the African Squirrels that approach *Xerus* in harshness of fur the skull and teeth are *Sciurus*-like, whereas those with softer fur approach *Xerus* in cranial characters.

In a paper upon the African Squirrels (Ann. Mag. Nat. Hist. (8) iii. pp. 467-475, 1909) Thomas revised de Winton's and Major's conclusions with respect to the Ethiopian species. As the result of a more exhaustive examination, he came to the conclusion, mainly on the evidence of skulls and teeth, that no fewer than twelve genera should be admitted:—*Sciurus* for *poensis* and two others; *Heliosciurus* for *gambianus*, *punctatus*, *rufobrachiatus*, etc.; *Myrsilus* for *aubinnii* and one other; *Funisciurus* for *isabella*, *leucostigma*, *lemniscatus*, etc.; *Paraxerus* for *cepapi*, *palliatu*s, *pauli*, etc.; *Protoxerus* for *stangeri* alone; *Epixerus* for *ebii* and *wilsoni*; *Atlantoxerus* for *getulus*; *Xerus* for *brachyotus* and *rutilus*; *Geosciurus* for *capensis*; *Euxerus* for *erythropus* and *microdon*; *Myosciurus* for *minutus*.

With the exception of *Myosciurus*, retained in the subfamily Nannosciurinae, all the rest were referred to the Sciurinae. But the genera of Sciurinae were divided into two sections, A and B, B containing the four genera *Atlantoxerus*, *Xerus*, *Geosciurus*, and *Euxerus*, distinguishable from the rest of the Sciurinae by their coarse fur and cranial characters.

In connection with these attempts to arrive at the truth with regard to the affinities of the species of Squirrels, it may be noted that both Forsyth Major and Thomas retained a certain number of typical African and Asiatic forms in the genus *Sciurus*, of which *S. vulgaris* is the type. This affiliation resulted from the evidence supplied by skulls and teeth; but the conclusion very forcibly suggested by the literature of the subject is the untrustworthiness of such characters.

This conclusion as applied to typical Squirrels was confirmed by Thomas in 1915 (Ann. Mag. Nat. Hist. (8) xv. pp. 383-387) from a study of the penis bone or *baculum*. To the details of this paper I shall refer in the following pages; but attention may here be drawn to one or two important points that were clearly brought to light:—(1) None of the tropical African * or Asiatic species, except *Rheithrosciurus*, shows any near affinity to *Sciurus*. (2) All the American Squirrels ranging from Canada

* To the African species assigned to *Sciurus* in 1909, Thomas subsequently gave the name *Æthiosciurus*, with *poensis* as the type (Ann. Mag. Nat. Hist. (8) xvii. p. 271, 1916), and in 1918 (Ann. Mag. Nat. Hist. (9) i. p. 33) he dismembered the black-striped species of *Paraxerus* from that genus, calling them *Tamiscus*.

to South Brazil are closely related to *Sciurus*. (3) The subfamily Nannosciurinae must be abolished as composed of heterogeneous elements, alike only in convergent characters*.

In 1923 (Proc. Zool. Soc. 1922, pp. 1171-1212) I published a paper on the external characters of all the species of Sciuridae available to me as fresh or spirit-preserved specimens. But for want of adequate material I was compelled to omit consideration of the penis and baculum. To Mr. Thomas's kindness in lending me the collection of bacula prepared under his orders at the Natural History Museum, I now owe the opportunity to figure and describe, not only the specimens of this bone described in general terms in his paper, but also those of a few Petauristidae, of *Citellus*, *Xerus*, and some others which he intended, granted time, to work out himself. To the account of these bacula I have added descriptions of the penis and bacula of such specimens of Sciuridae as I had preserved for the Zoological Society's collection.

DESCRIPTION OF THE PENIS AND BACULUM.

1. *The Palearctic and American Species.*

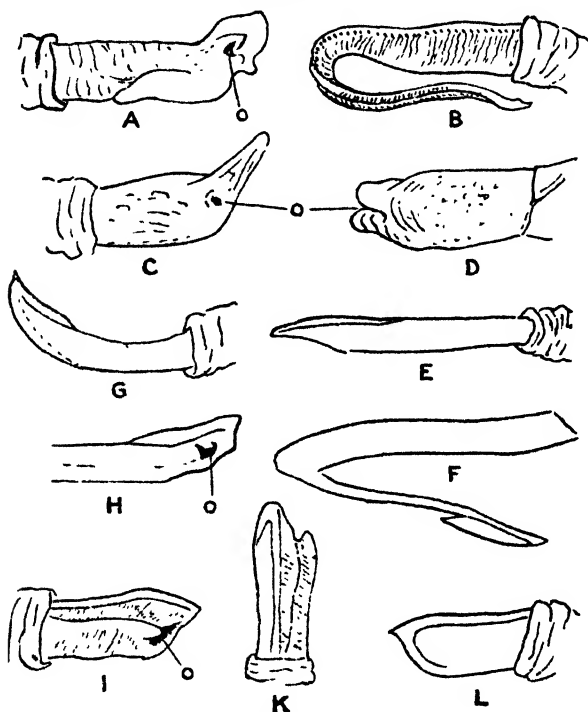
In *Sciurus vulgaris* the apex of the penis is compressed and upturned where the terminal blade of the baculum runs into it. The orifice opens on the right side behind and below the tip, and is surmounted by a small fleshy lappet; and the small process of the blade of the baculum forms a marginal projection just below and in front of the orifice. The soft swollen tissue enveloping the apex of the penis is continued backwards as a curved crest from above the orifice to terminate near the middle of the dorsal surface of the glans; and laterally and inferiorly it is defined by a groove from the wrinkled, more slender, and rod-like proximal portion of the glans. My observations on this species agree with those of Tullberg, who figured the penis and the extracted baculum from two points of view. (Text-figs. 18, A; 19, A, B.)

I find, moreover, that the glans penis of *Sciurus* (*Neosciurus*) *carolinensis* is of precisely similar structure. Thomas also described the baculum of *S. vulgaris*, and pointed out that the type of baculum found in that species occurs also in a number of other forms from Asia and North and South America. In the collection of the British Museum the bacula of the following species demonstrate this truth:—*S. vulgaris* from Europe, *persicus* from Asia Minor, *lis* from Japan, *niger* from North America, *carolinensis* from Tennessee and England (imported), *nayaritensis* from Jalisco in Mexico, *langedorffi* from the Sierra de Chapada, *ingrami* from Rio Janeiro, and *variabilis* from South America. And there is no reason to doubt that the glans penis in all these species conforms to the shape of the baculum. In view of these

* True at all events of the African *Myosciurus* and the Oriental *Nannosciurus*, which respectively fall into line with other species of the regions they inhabit. But the baculum of the South American genus has yet to be examined.

facts, Tullberg's statement that the North American species *Tamiasciurus hudsonicus*, always regarded as closely akin to the other Squirrels of that country and as ranking merely as a sub-genus of *Sciurus*, has an elongated apically attenuated glans penis

Text-figure 18.



- A. Glans penis of *Sciurus vulgaris*.
 B. The same of *Tamiasciurus hudsonicus*.
 C. The same of *Funambulus palmarum*.
 D. The same of *Tamiodon tristriatus*.
 E. The same of *Callosciurus prevosti*.
 F. Penis of the same, with baculum attached, showing position of blade.
 G. Glans penis of *Callosciurus notatus*.
 H. Apex of same from right side, showing orifice.
 I, K, L. The same of *Tomomys vittatus* from right side, above, and left side.
 o. Orifice.

without a baculum, appeared to me to be so remarkable and contrary to all expectations that I wrote to Mr. Gerrit S. Miller, of the Smithsonian Institution, Washington, to ask if he would be good enough to verify the statement for me. In reply, he very

kindly arranged for two male examples of the species, preserved in alcohol, to be sent to me*. From these two specimens I find that Tullberg was perfectly correct, and had not, as I supposed, made an error of identification. The glans penis in the Alaska specimen is slender and tolerably evenly tapering, with the orifice terminal and just beneath the apex. The upper surface has a median groove, and a pair of crests of minute serrulations running along it, and the sides are finely striolate. The distal portion below the bend is somewhat flattened, and provided on each side with a narrow laminate expansion. In the New York specimen, assigned to the subspecies *loquax*, the general form and sculpturing of the penis are much the same, except that the striolæ are coarser, the intervening spaces forming fine ridges, a difference possibly due to greater contraction of the epithelium, and the distal portion beyond the bend is not so evenly tapering, but shows an excrescence on each side. Nevertheless the two are of essentially the same type, and in both the distal portion is soft and flexible without a vestige of baculum that I can detect. The structure of the penis sharply differentiates *hudsonicus* from the Squirrels with the *vulgaris* type of penis and baculum, and compels the admission of *Tamiasciurus* as a well-defined genus without any near allies in the family. (Text-fig. 18, B.)

On the other hand, although Thomas stated that the baculum of the Bornean species *Rheithrosciurus macrotis* is like that of *Sciurus vulgaris*, he tells me that he is so impressed by the improbability, on geographical and other grounds, of the two species being alike in that respect†, that he considers confirmation of the fact necessary before definite acceptance be accorded it. There is always, of course, the possibility of confusion between the bones by taxidermists during the cleaning process.

The bacula of the *S. vulgaris* group are relatively well developed, but vary in size with the species, from about 14 mm. in *S. niger* to 8 mm. in *S. ingrami*.

The foregoing account shows that the Palearctic and American Squirrels fall into two categories by the structure of the penis and baculum:—

1. *Sciurus*, embracing the Palearctic species, all the Nearctic species except the one quoted below, and the Neotropical species.
2. *Tamiasciurus*, represented by *hudsonicus* and possibly related species.

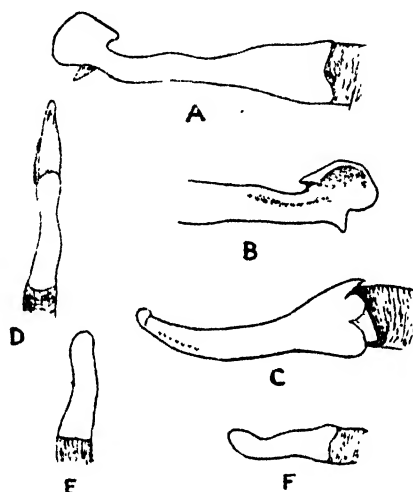
* My best thanks are due to the authorities of the Smithsonian Institution for the generous loan of these two Squirrels. One, in winter pelage (January), was collected at Nulato in Alaska by W. H. Dall, the other, in summer pelage (September), at Tamarak Swamp, New York, by E. A. Mearns.

† Although *Rheithrosciurus*, with its grooved incisors, has always been regarded as an isolated genus, the discovery that it is really related to *Sciurus* (s. s.), on the evidence of the baculum, would surprise me much less than did the discovery of the wide divergence between *Tamiasciurus* and *Sciurus* in the structure of the glans penis and the occurrence of the baculum.

2. *The Oriental Species.*

In *Funambulus palmarum* the glans is long, subcylindrical proximally, swollen and spongy in texture distally, and terminates in a longish, narrow, attenuated process, slightly or considerably inclined upwards and rising from the dorsal extremity of the swollen portion. The orifice lies at the base of this process at the right side. The baculum is a simple curved rod, concave on its upper side, convex below and tolerably gradually attenuated from the thick base to the narrow apex, which reaches to the extremity of the above-described terminal process of the glans. The

Text-figure 19.



- A. Baculum of *Sciurus* (*Parasciurus*) *niger*, from the left side.
- B. Apex of the same from the right side.
- C. Baculum of *Protoxerus stangeri*, from the left side.
- D. Baculum of *Funisciurus congicus*, from below, with the soft, dried, shrivelled tip of glans adherent.
- E. The same of *Paraxerus cepapi*, with the tip of glans removed.
- F. The same from the left side.

curvature varies apparently individually. The bone measures 10.5 mm.—that is to say, it is actually as long in this small Squirrel as in the giant *Ratufa*. (Text-figs. 18, C ; 20, D.)

In *Tamiodes* (gen. nov.) *tristriatus*, regarded by Blanford as possibly nothing but a local race of *palmarum*, the glans is very different. It is relatively shorter and thicker, and ends in two well-marked subequal labia, one above and one below the terminal orifice. The upper labium is unmodified ; but the lower, which has its inferior edge inclined upwards, is subdivided into a number of subordinate labia by deep lateral clefts, which are

represented on the lower side of the tip by grooves running obliquely backwards and inwards towards the middle line. It was clearly, I think, to a Squirrel of this genus, possibly indeed to *tristriatus*, that the glans penis figured and described by Tullberg as that of *palmarum* belonged. His figure, however, does not show such a definite lower lip as was present in the example from Malabar above described, the area beneath the upper lip being supplied with two rows of lobules representing the subdivisions of the lower lip in my specimen. (Text-fig. 18, D.)

The difference between *F. palmarum* and *T. tristriatus* in the structure of the penis is reflected in the shape of the baculum, which in *T. tristriatus*, instead of being gradually curved upwards from base to apex, has the proximal three-fourths curved towards the right with the right side concave, the left convex, and the distal fourth bent up at a right angle to form a vertical branch with an expanded tip, a convex crested posterior edge and a concave anterior edge. From the inferior angle of this arises a much smaller branch directed downwards. This description is taken from a baculum, measuring 11.5 mm., taken from a specimen of *tristriatus* from Helwak, Satara, and preserved in the British Museum. Another baculum in that collection, taken from an unidentified specimen without locality, differs in having a less expanded apex to the upper branch, no crest on the latter and no inferior branch, the shaft being straight. It measures 11 mm., and may represent a different race or species. (Text-fig. 20, A, B, C.)

In the example from Malabar of which the glans penis was described, the apex of the upper branch projected a little way into the upper lip of the glans, and the lower branch formed the bulge at the inferior part of the base of the lower lip. The baculum, measuring 12 mm., is similar in curvature and other particulars to that of the example from Satara, except that the inferior branch is more quadrate and not hook-like.

The two genera of Oriental Squirrels described above are a most instructive instance of close superficial resemblance associated with great differences in the glans penis and baculum. They are so much alike that Blanford was doubtful if *tristriatus* was more than what he would have called a "variety" of *palmarum*. Yet it is impossible to believe in close kinship between them; and the differences explain the occurrence of the two in the same districts in India without ever intergrading—that, at all events, I believe to be the case.

The structural characters of the two may be recapitulated as follows:—

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| <p>a. Glans penis ending distally in a narrow elongated point supported by the distal portion of the baculum; the orifice on the right side near the base of the slender portion and remote from the tip of the glans. Baculum a simple upcurved attenuated rod</p> <p>a'. Glans penis thick, blunted, and bilabiate distally, the orifice terminal between the upper and lower lips, the lower lip secondarily subdivided. Baculum with its terminal portion bent vertically upwards and curved forwards, with a prominent inferior angle</p> | <p><i>Funambulus.</i></p> <p><i>Tamiodes.</i></p> |
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The baculum of an example of *Ratufa gigantea* from Gokteik, N. Shan States, in the British Museum, is simple and shaped in a general way like that of *Funambulus palmarum*, but is relatively much shorter and stouter. It is expanded at the base, and in lateral view its upper and lower edges are respectively concave and convex, but with a sinuous outline. The distal end of the lower surface is irregularly bevelled up to the apex, which is narrowed but not pointed, and there are four subsymmetrically arranged rows of small irregularly spaced bony spicules on this distal portion, which from the dorsal or ventral aspect is seen to be slightly asymmetrical. It measures 10 mm. (Text-fig. 20, E, F.)

The baculum of a specimen, referred to the same species, from Darjiling is very similar, but more strongly bevelled and upcurved distally, the apex being a little expanded; and one of *R. fellii* from Yin, L. Chindwin, is also very like it. But a baculum of a captive specimen* of *R. indica*, without locality, also in the British Museum, is very different. It is a much larger and longer bone, about twice the length of the others if straightened, and has its distal half bent strongly upwards at an obtuse angle, a shoulder-like excrescence on each side marking the bend. This distal upturned portion is quite symmetrical, expanded basally and apically, concave laterally, hollowed inferiorly, and tridentate at the tip, the median tooth being a little longer and set further back than the laterals. This baculum, measuring in a straight line from base to apex 14 mm., may be perfectly normal. Its strongly upturned distal portion evidently corresponds to the slightly upturned denticulated, bevelled distal portion of the other bacula of the genus. (Text-fig. 20 G, H.)

Setting aside *Rheithrosciurus macrotis*, above referred to as probably having a baculum shaped like that of *Sciurus vulgaris*, the rest of the Oriental genera of Sciuridæ, as Thomas showed, have bacula specialised by the development, on the upper side, of a blade which is hinged to the shaft in such a way as to be slightly movable from right to left. The blade projects backwards, and a longer or shorter portion of its posterior end is free from the shaft. Bacula of this kind belong to two main categories—one, characteristic of *Callosciurus*, the other of *Tomeutes*. But distinct as the bacula of these two kinds are in their extreme forms, there are indications of intergradation between them†.

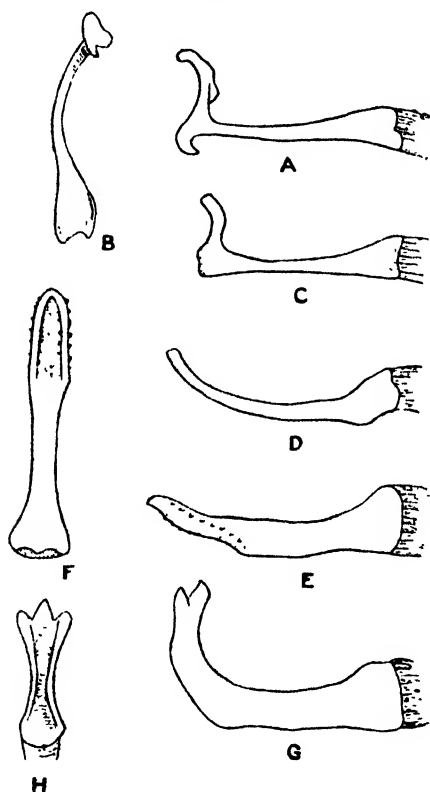
In *Callosciurus prerosti*, the type of *Callosciurus*, the glans is

* Bacula of mammals kept in confinement are sometimes abnormal.

† In his preliminary description of these bacula Thomas wrote:—"In position in the penis the blade points to the right, its edge cutting outwards." Again, the baculum of *Callosciurus* is said to have "a narrow blade set on the side of it, in the concavity of its general curvature . . . the greatest breadth [of the blade] is only about one-fourth to one-sixth of its length." This, however, does not agree with my observations, for I find in all the fresh or spirit-preserved material examined that the concavity of the shaft of the baculum and the blade are on the dorsal or upper side of the bone. If the blade were on the right side, the asymmetry of the baculum would be extreme and the edge of the blade would cut the right side of the vulva. I have no doubt that the function of the blade is to make a vertical cut of the integument (hymen) covering the orifice of the vagina.

long, slender, nearly straight and compressed, narrowed and pointed at the end, with the orifice just near the tip on the right side. There is comparatively little fleshy tissue enveloping the baculum, and the upper edge of the blade of the latter forms a

Text-figure 20.



- A. Baculum of *Tamiodes tristriatus*, from Satara, from the left side.
- B. The same from above.
- C. The same of another specimen, without locality.
- D. Baculum of *Funambulus palmarum*, from the left side.
- E. The same of *Rattus gigantea*, from the left side.
- F. The same from below.
- G. Baculum of captive specimen of *R. indica*, from the left side.
- H. Distal end of the same, from the front.

hard, sharp ridge, covered merely by a coating of fine membrane, at the distal end of the dorsal side of the glans. The baculum itself is long and slender, gradually attenuated from base to point and with a sinuous curvature, being slightly concave in the

middle below and above in its distal third. The blade, about one-third of the length of the entire bone, is lodged in the distal concavity. It has a straight upper edge, not rising above the median dorsal convexity of the shaft. Its posterior third is pointed and free from the shaft. Its anterior end is attached immediately behind the slightly expanded tip of the shaft. Hence the blade is at the distal end of the shaft. The baculum above described measures 26 mm., the longest in the Sciuridæ. (Text-figs. 18, E, F; 21, B.)

Callosciurus notatus, from Java, has the glans shorter than in *C. prevosti* and with a pronounced dorsal curvature in its distal half, so that its upper surface is concave, its lower surface convex. The sharp distal edge formed by the blade is more pronounced, and the orifice is situated as in *C. prevosti*. The baculum differs from that of *C. prevosti* in being relatively stouter, in having a larger thickening at the proximal end, a strongly upcurled distal half with a concave upper and a convex lower edge; but the blade, although similarly placed distally, is not so pointed and its upper edge is above the line of the edge of the shaft preceding it. (Text-figs. 18, G, H; 21, C.)

In specimens of *C. castaneiventris* from Ningpo and of *C. atrodorsalis* from Siam the shaft of the baculum resembles that of *C. notatus*, although it is less strongly curved upwards; but the blade, which is considerably longer, being nearly half the length of the shaft, is not attached to its distal end, which projects freely beyond the anterior end of the blade, the blade itself lying nearly in the middle of the dorsal concavity of the shaft. In *C. castaneiventris* the baculum measures 19 mm. (Text-fig. 21, A.)

In Thomas's preliminary account of the bacula of the Oriental Squirrels, *C. prevosti* was one of the species in the list of unexamined forms, whereas *C. notatus*, *castaneiventris*, and *atro-dorsalis* appear in the list of species of which the baculum was examined. The remaining species of this list were *caniceps*, *erythræus*, *pluto*, and *sladeni*.

The differences between the bacula of *C. prevosti* and *C. notatus* on the one hand and of *C. castaneiventris* and *C. atrodorsalis* on the other suggest the possibility of usefully splitting *Callosciurus* into two genera. The characters appear to me to be at least as valuable as the presence or absence of a degenerate premolar. But it would perhaps be premature to take that course, at all events until it has been shown that the bacula of other species do not show intermediate stages in the position of the blade.

The baculum of a specimen of *Menetes berdmorei* from Kokareet (Tenasserim) in the British Museum very closely resembles that of *C. prevosti* described above, except that the shaft is straight up to the concavity containing the blade. It is convex below only at its distal end and correspondingly concave above, the blade lying in the distal concavity as in *C. prevosti* and *C. notatus*. The baculum of this species, measuring 11 mm., was held by Thomas to have a blade somewhat connecting the types of bacula

characteristic of *Callosciurus* and *Tomeutes*. It does not seem to me that its baculum is more *Tomeutes*-like than that of *C. notatus*. The partial intergradation between the bacula of *C. prevosti*, the type of *Callosciurus*, and of *T. lokroides*, the type of *Tomeutes*, is effected, as explained below, by *C. notatus* and *T. vittatus*. (Text-fig. 21, D.)

The bacula of what may be called the *Tomeutes* type differ from those of the *Callosciurus* type above described in having the shaft of the bone shorter and thicker, and the blade deeper and longer, with a shorter hinged area and a longer portion free from the shaft. The shaft is variable in length, being sometimes twice the length of the blade, the point of which falls considerably short of its proximal end or base, or sometimes a little shorter than the blade, the point of which then overlaps the base of the shaft. In all cases probably the glans penis is shorter and thicker than in *Callosciurus*.

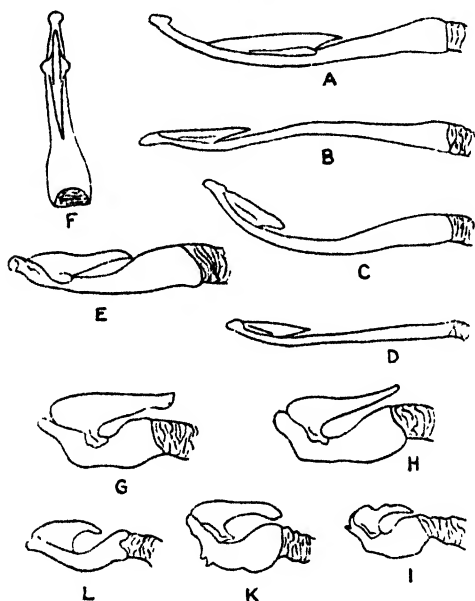
In *Tomeutes vittatus* the glans penis is very like that of *Callosciurus notatus*, but is relatively shorter and thicker. Its upper and lower edges are parallel; along its upper runs a sharp carina formed by the edge of the blade of the baculum and ending distally in a short point. On the right side about half-way between this point and the inferior rounded angle of the distal end opens the orifice, which has a little fleshy lobe on its outer side; and from this a groove runs backwards along the right side of the glans nearly to its proximal end. (Text-fig. 18, I, K, L.)

The baculum, measuring 14 mm., although conforming in a general way to the typical *Tomeutes* type of baculum, is more like that of *Callosciurus notatus* than any I have seen. The shaft is about twice the length of the blade, very thick at the base, slender beneath the blade, with lightly convex but sinuous inferior border, and upturned at the apex, which is furnished with a small button-shaped thickening projecting an appreciable distance beyond the distal end of the blade. The latter, lying in the concavity of the upper side of the shaft, has a nearly straight, smooth upper edge, the lower edge, also nearly straight, running obliquely upwards and backwards to meet it in a point. The hinged portion ends inferiorly in an expansion on each side which, as it were, clamps the blade to the shaft, and corresponds to the lateral expansion of the blade seen in *Callosciurus notatus* and *castaneiventris*. This species, *Tomeutes vittatus*, appears in Thomas's list of unexamined species of *Callosciurus*. From the superficial resemblance between *vittatus* and *notatus*, he probably inferred that their bacula would be alike. That, however, is not the case. (Text-fig. 21, E, F.)

The baculum of a specimen of the type of the genus *Tomeutes*, namely *T. lokroides*, from Kursiong in Sikkim, preserved in the British Museum, has a much shorter shaft and bigger blade than that of *T. vittatus*, and is altogether more specialised. The shaft has a thickened proximal end with the distal third sharply upturned, making a deep, short concavity. The blade, measuring

8 mm., is longer than the shaft, its blunted point overlapping the thickened proximal end of the shaft, and the upper edge of the blade rises high above the concavity of the bone. In this respect it differs from the baculum of *T. vittatus*, where the upper edge of the blade does not project above the concavity lying between the apex and base of the shaft. (Text-fig. 21, G.)

Text-figure 21.



- A. Baculum of *Callosciurus castaneiventris*, from the left side.
- B. The same of *C. przewalskii*.
- C. The same of *C. notatus*.
- D. The same of *Moneile berdmorci*.
- E. The same of *Tomomys vittatus*, from the left side.
- F. The same from above.
- G. The same of *T. lokroides*, from the left side.
- H. The same of *T. hippurus*.
- I. The same of *T. robinsoni*.
- K. The same of *T. miniatus*.
- L. The same of *T. tahan*.

The baculum of a specimen of *T. hippurus* from Bukit Tangga, Negri Sembilan, also has the blade overlapping the proximal end of the shaft, but not to the same extent as in *T. lokroides*. The shaft, moreover, is relatively longer, with a longer concavity; the blade is not so deep and does not project so high above the concavity of the baculum as in *T. lokroides*. In a measure this

baculum serves to connect those of *T. vittatus* and *T. lokroides*. (Text-fig. 21, H.)

The baculum of a specimen of *Tomeutes miniatus* from Bukit Kutu, Selangore, has the shaft tolerably similar to that of *T. lokroides*, but the blade is slightly shorter than the shaft and much thinner, being concavely emarginate inferiorly so that there is a larger space between its lower border and the subjacent upper edge of the shaft. There are also a few bony spikes on the inferior edge of the shaft at the base of the upturned distal portion. The bone measures 7.5 mm. This species, Mr. Thomas tells me, comes near *T. vittatus* in general characters; but the great differences in their bacula preclude the view of close kinship between the two species. (Text-fig. 21, K.)

In a specimen of *Tomeutes robinsoni*—a species akin, Mr. Thomas tells me, to *T. lowii*—from Bukit Tangga, Negri Sembilan, the baculum has the shaft short, stout, and strongly curved, being very like that of *T. miniatus* but somewhat thicker proximally, shorter, and without trace of the bony spicules. The blade, too, is tolerably similar but shorter, with a lightly convex upper edge, with a notch and tooth. The bone measures 6 mm. (Text-fig. 21, I.)

In a specimen of *T. tahan* (allied to *T. tenuis*), from Bukit Kutu, Selangore, the shaft is relatively longer and thinner than in the previously described species, except *T. vittatus*, and its inferior angle, very obtuse, is near the middle of the lower surface approximately beneath the point of the blade. The blade itself is short and deep, with a long hinge, a lightly convex upper edge, a strongly concave lower edge, and a narrow apex. The bone measures 5 mm. Judging from the baculum alone this species would be referred to *Dremomys*. (Text-fig. 21, L.)

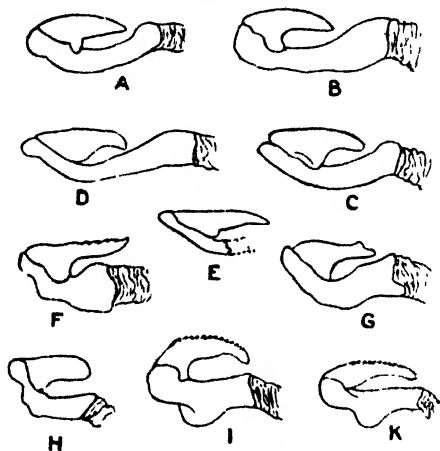
The main distinctive features of the bacula of the species of *Tomeutes* above described may be summarised as follows:—

- a. Shaft comparatively long, about twice as long as blade, its lower edge lightly convex, its apex projecting well beyond blade; upper edge of blade not higher than line tangential to upper proximal and distal ends of shaft *vittatus*.
- a'. Shaft comparatively short, much less than twice as long as blade, its lower edge strongly curved or geniculate, its apex only surpassing blade slightly; upper edge of blade higher than line tangential to upper proximal and distal ends of shaft.
- b. Angle of lower edge of slender shaft set far back almost beneath point of blade, distal portion beyond bend inclined gradually upwards; hinge nearly as long as blade *tahan*.
- b'. Lower edge of stout shaft with pronounced angle in front of lower end of hinge, distal portion beyond angle tipped steeply upwards; hinge much shorter than blade.
- c. Blade with apex not overlapping proximal end of shaft, its lower edge deeply and widely emarginate towards hinge ... *miniatus, robinsoni*.
- c'. Blade with apex overlapping proximal end of shaft, its lower edge nearly straight up to small concave notch by hinge. *lokroides, hippurus*.

According to Thomas the following species belong to *Tomeutes*:—*phayrei*, *blanfordi*, *pygerythrus*, *janetta*, *pryeri*,

philippinensis, *melanogaster*, *tenuis*, *brookei*, *lowii*, *murinus*. I have not seen their bacula; but those described above are sufficient to show how variable this bone is within the limits of the genus as admitted by Thomas. The variation, indeed, is so great that it is impossible to affirm any character by which the baculum of *Tomeutes* can be distinguished from the bacula of *Dremomys*, *Rhinosciurus*, *Tamiops*, and *Lariscus*. It is not improbable that a careful comparison between the bacula of all the species assigned at present to *Tomeutes* will give useful indication of interspecific relationship.

Text-figure 22.



- A. Baculum of *Dremomys lokriah*, from the left side.
- B. The same of *D. rufigenis*.
- C. The same of *D. rufigenis fuscus*.
- D. The same of *D. dawsoni*.
- E. The same of *Lariscus jalorensis*.
- F. The same of *Rhinosciurus robinsoni*.
- G. The same of *Tamiops maclellandi barbei*.
- H. The same of *Nannosciurus microtis*.
- I. The same of *N. whiteheadi*.
- K. The same of *N. exilis*.

The baculum of a specimen of *Lariscus jalorensis* from Bukit Tangga, Negri Sembilan, is represented by the blade and the piece of the shaft to which it is attached. This portion of the blade is compressed and shows no angulation of its inferior border, which suggests that the upcurvature was gradual as in *Tomeutes vittatus* or *Dremomys dawsoni*. Its apex is produced as an acute angle beyond and in the same line as the upper edge of the blade, which is nearly straight, with a slightly depressed apex, and forms an acute angle with the line of the hinge very

much as in *Tomeutes vittatus*. In the latter, however, the apex of the shaft is expanded and button-shaped, not compressed as in *Lariscus jalorensis*. (Text-fig. 22, E.)

The baculum of a specimen of *Rhinosciurus robinsoni* from Tiernan Island, in the British Museum, is very like that of *Tomeutes lokroides*. The shaft is short, proximally thick, distally upturned, with a short concavity, with its large blade projecting high above it and overlapping the proximal end. The upper edge of the blade is nearly straight, but is irregularly notched in its posterior half. The bone measures 10 mm. (Text-fig. 22, F.)

In a specimen of *Tamias maclellandi barbei* from Kokareet, in the British Museum, the shaft of the baculum gradually narrows from base to apex, its distal half being upturned at an obtuse angle. The blade has a long hinge but is short, the point being very narrow, with a notch and tooth near its apex. Its upper edge is only slightly higher than a line touching the upper edge of the proximal and distal ends. The bone measures 5 mm. (Text-fig. 22, G.)

In four species of *Dremomys*, namely, *D. lokriah* from Sikkim, *D. rufigenis* from H'Kauti, Chindwin, *D. rufigenis fuscus* from Annam, and *D. dawsoni* from Tatken, Chindwin, the shafts of the bacula are longish and longer than the blades. In that of *D. rufigenis* the proximal end of the shaft is very thick and raised, the median part is straight, and the upcurved distal end has an evenly convex edge. The upper edge of the blade is markedly convex to the apex, which falls far short of the proximal end of the shaft; its lower edge is straight with a pronounced concavity near the hinge. The baculum of *D. rufigenis fuscus* is sufficiently different to suggest specific distinction between the two forms. The shorter shaft is comparatively narrow proximally, its inferior edge is evenly convex, the upcurvature beginning beneath the inferior end of the hinge; the blade is larger as compared with the shaft, has a longer hinge, an evenly concave lower border, and a less convex upper border. In *D. dawsoni* the shaft overlaps the blade proximally to an even greater extent than in *D. rufigenis*, but it is not so stout, and its lower edge is inclined upwards from a point below the inferior end of the hinge as in *D. rufigenis fuscus*, but more abruptly, and the concavity of the lower edge does not extend up to the bottom of the hinge, the edge at this point being slightly convex. In *D. lokriah* the shaft is very like that of *D. rufigenis fuscus*, but is a little stouter distally, and the lower edge of the blade is straight up to the point where it runs into the thickening forming the lower end of the hinge. (Text-fig. 22, A-D.)

The bacula of the species of *Dremomys* above described may be contrasted as follows:—

- a. Lower edge of shaft tolerably straight for the greater part of its length, distal end of shaft expanded with strongly rounded edge; blade thinner, with wide emargination close to short hinge *rufigenis*.

- a'*. Lower edge of shaft tolerably evenly convex throughout or convex beneath lower end of long hinge, distal end not expanded, without strongly convex edge.
- b*. Apex of blade some distance from proximal end of shaft, lower edge of blade with sigmoid curvature... .. *dawsoni*.
- b'*. Apex of blade a little behind proximal end of shaft, lower edge of blade without sigmoid curvature.
- c*. Lower edge of blade evenly emarginate, distal end of shaft not thickened *rufigenis fuscus*.
- c'*. Lower edge of blade straight up to angular notch by hinge; distal end of shaft to which blade is hinged somewhat expanded *lokriah*.

In three species of *Nannosciurus*—*N. whiteheadi* from Kina Balu, *N. exilis* from Borneo, and *N. microtis* from Sarawak—the proximal end of the shaft of the baculum is not thickened and elevated, and its upper edge, as far as the hinge of the blade, is almost straight, and is parallel in a general way to the lower edge of the blade; the tip of the blade just reaches the base of the shaft. In *N. whiteheadi* and *N. exilis* the lower side of the shaft has a rounded swelling near the middle, and the distal end is only a little raised; the blade is arcuate with serrated upper edge and a narrowed point. In *N. whiteheadi* the apex of the shaft, to which the blade is hinged, is thicker, and the blade itself is more arcuate and more strongly serrated than in *N. exilis*. In *N. microtis* the shaft has no definite inferior thickening, its distal half is bent up at an obtuse angle, the blade is not arcuate nor serrate, and the tip is bluntly rounded and scarcely narrowed in profile view. (Text-fig. 22, H-K.)

The measurements of these bacula are as follows:—*N. whiteheadi* 5 mm., *N. exilis* 4 mm., *N. microtis* 3 mm.

In the following table the characters of the bacula of the three species of *Nannosciurus*, here described, are briefly summarised:—

- a*. Shaft with its distal half bent up at an obtuse angle without a rounded thickening near the middle of its lower surface; blade with tolerably straight, smooth upper edge and widely rounded tip *microtis*.
- a'*. Shaft tolerably straight axially from end to end, the extreme apex a little elevated, a conspicuous thickening near the middle of the lower surface; the blade long, apically attenuated, with upper edge convex and serrulate.
- b*. Blade high and arched, with wide space between its lower edge and the shaft... .. *whiteheadi*.
- b'*. Blade lower, less arched, a much narrower space between its edge and the shaft *exilis*.

The Oriental Squirrels thus fall into three main groups, judged by their bacula:—

1. *Rheithrosciurus*, belonging to the same group as *Sciurus* of the preceding section.
2. *Ratufa*, *Funambulus*, and *Tamiodes*, with simple bacula.
3. *Callosciurus*, *Tomeutes*, *Tamiops*, *Lariscus*, *Nannosciurus*, etc., which have compound bacula provided with a blade.

3. *The Ethiopian Species.*

In *Protoxerus stangeri*, as identified by Tullberg, the glans penis is elongated and nearly straight, but exhibits at the distal end of its proximal half a large swelling, showing a pair of low crests above and a pair of distally directed pointed processes below. Beyond the swelling the glans is gradually narrowed towards the apex, but the apex itself is shaped like an arrow-head, with the point slightly upturned and a pair of small swellings just before it. (Text-fig. 23, M.)

The baculum of a specimen of this species from the Como River, in the British Museum, is a symmetrical bone, slightly concave above, convex towards the middle below, a little upturned at the apex, which ends in a blunt condyle-like button. On each side of the shaft in its distal third towards the apex there is a faintly defined longitudinal crest. The proximal end, or base, is much thickened, and carries a coronet consisting of five symmetrically arranged bony lobes, one being in the middle line above and two on each side, the two lower lobes being separated by a notch in the middle line below. There is no doubt, I think, that the thickened proximal end of this bone is imbedded in the tissue forming the submedian thickening of the penis described and figured by Tullberg, and, from analogy, I suspect the button-like tip of the baculum is lodged in the thickened portion of the arrow-headed apex. (Text-fig. 19, C.)

The actual length of the bone, despite the large size of the Squirrel, is 7.5 mm.

In *Ethosciurus poensis*, as identified by Tullberg, the glans penis is quite short, and consists of a thickened proximal portion, composed of two transverse folds of soft tissue of which the posterior has a finely serrated posterior border on the upper side, and of a slender distal portion which gradually narrows from the base to the simple apex. According to Tullberg, the glans penis of this species has no baculum, but from analogy I suspect a small baculum, imbedded in the tissues, was overlooked.

In an example of *Funisciurus leucostigma* from Bibianaha the glans penis is not at all unlike that of *E. poensis*. Its proximal portion is quite short and thick, consisting of soft grooved tissue, but the distal portion, abruptly differentiated from the proximal, is a comparatively slender somewhat flexible rod, tapering apically but furnished on each side with a serrulated crest starting distally behind the tip and ending proximally on the upper side of the thickened base. These two crests define the upper from the lateral surfaces of the process. (Text-fig. 23, E-G.)

In *Funisciurus leucostigma niveatus* the glans penis differs somewhat from that of *F. leucostigma* above described, although consisting of a short undifferentiated proximal portion, a swollen laminate and grooved median portion, and a thinner longer distal serrulated flexible portion. The median portion, however, is not so thick as in typical *F. leucostigma*, and the distal portion is

thicker and more irregular in shape, being markedly asymmetrical and not so sharply marked off from the swollen median portion. The orifice appears to lie in the swollen median portion beneath the proximal end of the distal portion. When at rest within the abdomen the terminal half of the distal portion lies in the prepuce and is bent like a hook, and the penis does not extend beyond the prepuce as in *Heliosciurus rufobrachium* described below. (Text-fig. 23, C, D.)

The dried distal portion of the glans of a specimen of *Funisciurus pyrrhopus* from Ashanti, in the British Museum, agrees in all essentials with that of *F. leucostigma*, except that the apex is better defined and more like an arrow-head. The baculum, a simple rod measuring about 1.5 mm., is imbedded in the serrulated area, its distal end not reaching the tip of the glans.

In a similarly preserved part of the glans of *F. congicus*, with the tissue of the serrulated area cut away leaving the baculum exposed, the baculum is a slightly curved rod about 2 mm. in length, and the dried tissue of the apex of the glans, still attached to the distal end of the baculum, is lanceolate. (Text-fig. 19, D.)

In *Paraxerus cepapi* the glans is very similar to that of *Funisciurus leucostigma*. The proximal portion is very thick and short, and bent on itself, its convex surface having a median line of serrulations. Distally this thickened portion shows grooved flaps of soft tissue. The terminal process is very like that of *Funisciurus leucostigma*, being broad at the base, pointed at the apex, and provided dorso-laterally on each side with a serrulated crest. The sides of this process are, however, concave, so that the dorsal area bordered by the crests is much narrower in the middle than behind and in front. (Text-figs. 23, H, I; 19, E, F.)

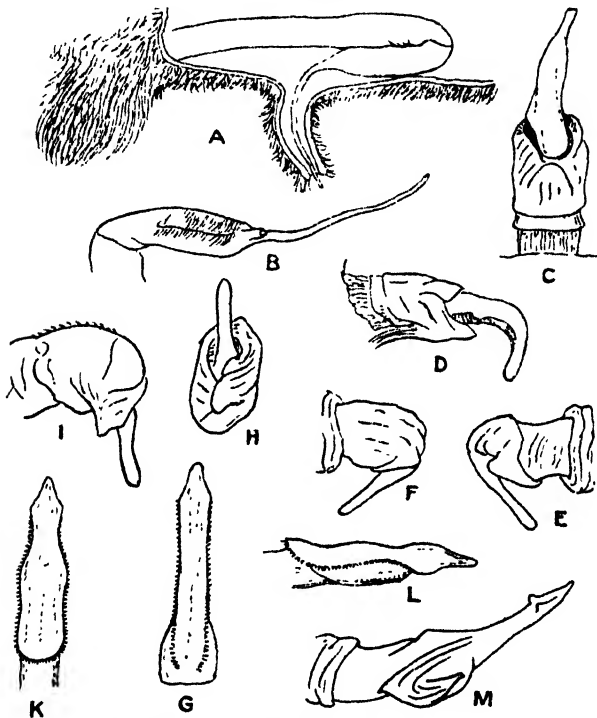
The dried process of the glans of a specimen of *Paraxerus palliatus* from Zululand, in the British Museum, is tolerably similar, but the serrulated area is somewhat sharply constricted in front, so that the tip of the process is better defined and more arrow-headed in shape and the middle of the serrulated area is broad, broader indeed than its proximal end, where it rises into a crest. The baculum, measuring less than 2 mm., is imbedded in the process of the glans behind the apex and between the constrictions. (Text-fig. 23, K, L.)

The dried condition of the distal portion of the glans penis of *Funisciurus pyrrhopus* and of *Paraxerus palliatus* makes their comparison with that of the spirit-preserved material of *F. leucostigma* and *Paraxerus cepapi* a little unsatisfactory. But the general similarity between the penes of these two so-called genera admits of no doubt. I suspect Tullberg overlooked both the baculum and the serrulated crests in the specimen he referred to *Sciurus poensis*.

In an adult male of *Heliosciurus rufobrachium hardyi* the penis is of exceptional length. When extended it reaches as far as the posterior end of the sternum, and measured from its

origin just in front of the anus, it is more than half the length of the head and body. Within the abdomen its proximal portion up to the origin of the glans projects some distance beyond the prepuce. The glans is very sharply divided into two parts, a

Text-figure 23.



- A. Penis of *Heliosciurus rufobrachium hardyi*, retracted.
 B. Glans of the same extended, from the right side.
 C. Glans penis of *Punisciurus leucostigma niveatus*, from above.
 D. The same from the right side.
 E. Glans of *F. leucostigma*, from the left side.
 F. The same from the right side.
 G. Narrowed distal portion of the same, from above.
 H. Glans of *Paraxerus cepapi*, from above.
 I. The same from the right side.
 K. Narrowed distal portion of glans of *Paraxerus palliatus*, from above.
 L. The same from the right side.
 M. Glans of *Protoxerus stangeri*, from right side (after Tullberg).

proximal and a distal, nearly equal in length. The proximal portion, when at rest, is folded back beneath the distal end of the preglandular part of the penis, is dorso-ventrally expanded, and

slightly compressed and striolate laterally. Its upper portion is lightly convex, smooth, and cartilaginous, but not ossified. Its lower portion consists of softer tissue, and carries the urethral orifice on a small fleshy process at the distal extremity of its right side. The distal extremity of the glans is long, slender, flexible, and filiform, like a rat's tail. I can find no trace of baculum in it, unless the remnant of this bone is represented by a slight opacity at the distal end of the thread. (Text-fig. 23, A, B.)

In an immature male of *Heliosciurus punctatus* the penis resembles in a general way that of *H. rufobrachium*, being exceedingly long and distally slender and filiform without trace of baculum. The specimen is not well preserved, but the filiform portion appears to terminate in a small arrow-headed tip and to pass into the main body of the penis without the intervention of the swollen glandular portion carrying the orifice such as is seen in *H. rufobrachium*. The position of the orifice I could not determine.

The differences above described are very considerable, and if they are found to obtain in adult examples of *H. punctatus*, they would, I suppose, indicate a generic difference between that species and *H. rufobrachium*. But since the example in question is immature and poorly preserved, the examination of fresh material must be awaited ere a decision on the point is reached.

Temporarily setting aside the penis of the example of *Heliosciurus punctatus* above described, the characters of this organ as shown in the other genera may be tabulated as follows:—

- a. Penis exceedingly long, the distal portion of the glans forming a long, flexible thread-like termination without baculum *Heliosciurus*.
- a' Penis quite short; the distal portion of the glans shorter, stouter, rod-like, not filiform, and provided with a baculum.
- b. The narrow rod-like distal portion flexible, with a finely serrulated crest on each side, and carrying a minute baculum near its distal end *Ethosciurus*, *Funisciurus*, *Paraxerus*.
- b' The narrowed distal portion not flexible, without serrulated crests, but supported throughout by a relatively large baculum. *Protoxerus*.

It must be remembered, however, that the characters assigned to the penis of *Protoxerus* and *Ethosciurus* are taken from Tullberg's descriptions and not from my own observations.

Despite the differences between the penes of these genera, there are certain significant features they have in common. The glans is divisible into two parts, a swollen proximal portion carrying the urethral orifice and a more slender terminal portion.

The most primitive type appears to be that of *Protoxerus*, where the terminal portion is relatively stout, moderately long, less sharply distinguished from the swollen proximal portion, without serrulated crests, and supported by a well-developed baculum, the proximal thickened end of which is probably lodged in the thickening of the glans, while the apex extends to the arrow-headed tip of the thinner distal portion.

In the next stage, exemplified by *Ethosciurus*, *Paraxerus*, and

Funisciurus, the baculum is reduced to a small rod imbedded near the apex of the distal portion, which is consequently flexible. This portion, however, is specialised by the development of a finely serrulated crest on each side, and is more sharply marked off from the swollen portion of the glans, upon which it is capable of being moved up and down.

Finally in *Heliosciurus*, the highest type, the distal portion is developed into a flexible filiform process without baculum, the thickened portion of the glans is longer and simpler, and the preglandular portion of the penis is greatly lengthened.

Returning to *Protoxerus*, it may be recalled that Thomas drew attention to the likeness between its baculum and the baculum of *Ratufa*. Unfortunately the penis of *Ratufa* is unknown; but a similarity may be traced between the glans of *Protoxerus* and of *Funambulus* if, as I suppose, the orifice opens in *Protoxerus* on the swollen part of the glans at the base of the terminal slender portion. The chief differences in that case between them will be reduction in the size of the baculum in *Protoxerus* and specialisation of the glandular thickening from which the slender terminal portion arises. In any case the likeness between the bacula and penes of *Protoxerus* and *Funambulus* is greater than the likeness between those same organs in *Funambulus* and *Tamiodes*.

4. The African Ground-Squirrels.

In the African Bristly Ground-Squirrels the glans penis is relatively large, turns downwards at the apex, and has a well-developed terminal baculum.

In *Euxerus erythropus* the glans is long, and consists of two parts, a subcylindrical proximal piece composed of soft, striate or otherwise sculptured tissue, and a terminal smooth, compressed piece with an elevated, convex upper edge which curves downwards distally to end in a rounded apex, behind which the inferior border is concave. The upper edge ends posteriorly in a twist near the middle of the upper side of the glans. At the distal end of the spongy portion beneath and a little to the right of the middle line just behind the base of the compressed portion, the orifice opens. (Text-fig. 25, E-H.)

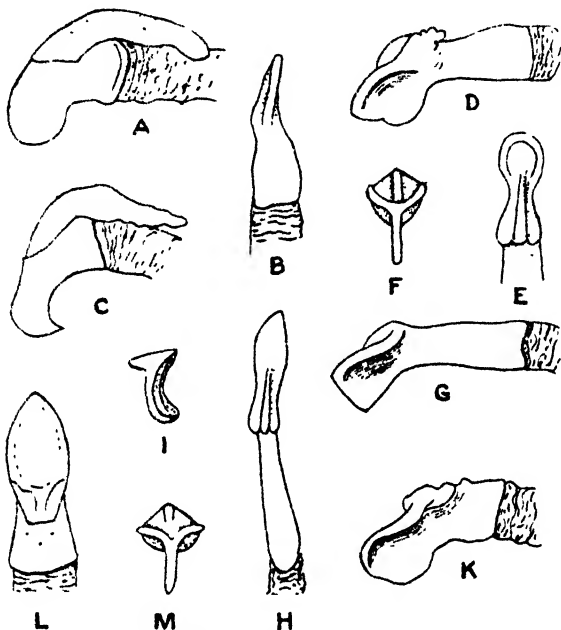
The baculum, measuring 8-9 mm., conforms to the shape of the distal portion of the glans, and consists of a stout, short cylindrical proximal piece and a compressed blade, sometimes rounded, sometimes hooked backwards at its inferior apex. The upper side of the bone is slightly concave; but carries a cartilaginous crest, sometimes partially ossified, which runs backwards some distance behind the proximal end of the bone and represents the distal dorsal crest of the glans. (Text-fig. 24, A-C.)

The glans of *Geosciurus capensis* is tolerably similar, with a similar dorsal crest ending in a twist proximally, but the distal portion is not compressed, but gradually narrows to end in a

slightly expanded truncated apex. The orifice is in the median ventral line, nearer the tip of the glans than in *Euxerus erythropus*. (Text-fig. 25, A-D.)

The baculum, measuring 8 mm., has a much longer proximal subcylindrical portion than that of *Euxerus*, and the upper

Text-figure 24.

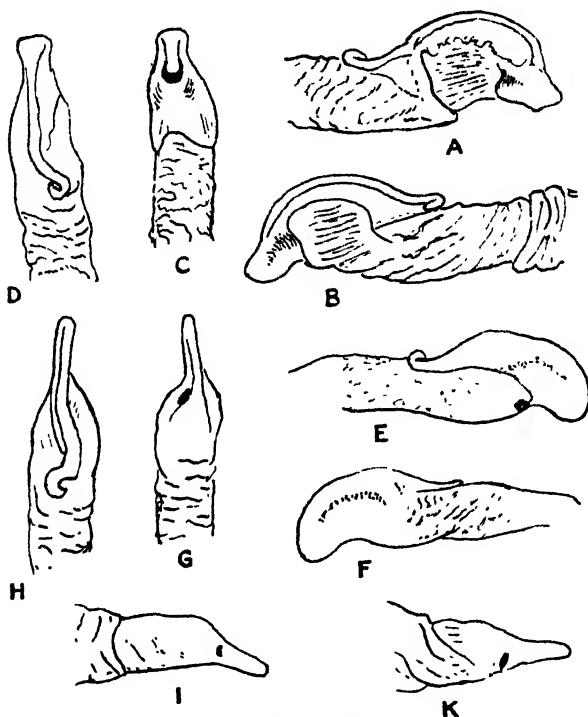


- A. Baculum of *Euxerus erythropus*, from the left side.
- B. The same from above, without the cartilaginous crest.
- C. Baculum of another specimen, ticketed *E. erythropus*.
- D. Baculum of *Geosciurus capensis*, from the left side.
- E. Apex of the same from above.
- F. Apex of the same from the front.
- G. Baculum of *Atlantoxerus getulus*, from the left side.
- H. The same from above.
- I. Tip of the same from the front.
- K. Baculum of *Xerus rutilus*, from the left side.
- L. The same from above.
- M. Tip of the same from the front.

surface of the terminal portion is an elongated area rather more than twice as long as broad, with a low median crest, a rounded spatulate hollowed apex, and distinctly constricted sides. The lower side of the terminal portion is developed into a median vertical crest. (Text-fig. 24, D-F.)

The baculum in *Atlantoxerus getulus*, measuring 7 mm., has a still longer proximal portion, or "handle," than in *Geosciurus*, and the blade is simpler. Its dorsal area is apically asymmetrical and not markedly spatulate, and the sides are scarcely constricted,

Text-figure 25.



- A. Glans penis of *Geosciurus capensis*, from the right side.
- B. The same from the left side.
- C. The same from below.
- D. The same from above.
- E. The same of *Euxerus erythropus*, from the right side.
- F. The same from the left side.
- G. The same from below.
- H. The same from above.
- I. The same of *Cynomys ludovicianus*, from the right side.
- K. The same of *Marmota marmota*.

but the median crest seen in *Geosciurus* is present. The inferior crest of the blade is also asymmetrical, curving towards the left inferiorly. (Text-fig. 24, G-I.)

In *Xerus rutilus* the "handle" of the baculum is shorter than

in *Geosciurus* and no longer than in *Euxerus*; but the upper surface of the blade is very wide, much wider than the "handle" and shaped like a spearhead, with convexly rounded sides and a sharp point, the width being rather more than half the length; its dorsal median crest is much less pronounced than in *Geosciurus* and its apex is not spatulate and hollowed. The inferior crest is similar to that of *Geosciurus*. The bone itself measures 6 mm. (Text-fig. 24, K-M.)

Of the above-described bacula that of *Atlantoxerus* comes nearest to the baculum of typical Sciuridæ in the length of the proximal cylindrical portion or handle; *Geosciurus* comes next, and *Xerus* and *Euxerus* last with the proximal portion quite short. In the gradual differentiation or specialisation of the blade the series runs *Euxerus*, *Atlantoxerus*, *Geosciurus*, *Xerus*; but which of the four is the most primitive type I am quite unable to say. It is interesting, however, to note that the most widely separated types are found in *Xerus* and *Euxerus*, which until recently were referred to a single genus, although *Geosciurus* and *Atlantoxerus* had been severed from *Xerus*.

- | | |
|---|-----------------------|
| a. Distal portion of baculum a compressed blade not expanded above, its upper edge narrow | <i>Euxerus</i> . |
| a . Blade of distal portion of baculum laterally expanded more or less above, its upper surface spatulate or subs spatulate with a longer or shorter median crest behind. | |
| b. The upper surface forming an elongated oval plate with uniformly convex sides, pointed at the apex and with a short crest behind; proximal portion of baculum only about half the length of the distal | <i>Xerus</i> . |
| b'. The upper surface much narrower, with sinuous sides and a longer crest; proximal portion almost as long as the distal or longer. | |
| c. Sides of the upper surface strongly constricted, the terminal area apically rounded and hollowed | <i>Geosciurus</i> . |
| c'. Sides of the upper surface weakly constricted, the terminal area apically narrow and flat | <i>Atlantoxerus</i> . |

A point of systematic interest connected with the glans penis and baculum of the Xerinae is the complete absence of resemblance between them and the corresponding organs in the African Squirrels, *Protoxerus*, *Funisciurus*, and *Paraxerus*, which were associated with *Xerus* by Forsyth Major on the evidence derived from skulls and teeth.

5. The *Sousliks* and *Marmots*.

The glans penis of *Citellus* I have had no opportunity of examining, but the bacula of several species are preserved in the collection of the British Museum. In all cases the bone consists of an elongated shaft, broad at its proximal end and narrowing distally to the apex, which is upturned and expanded into a wide, sometimes double disc with denticulated margin.

The simplest type is the baculum of a specimen of *C. mongolicus* from Chifu. The shaft is abruptly expanded at the base,

nearly straight when viewed from above or below, but with the upper margin concave, the lower convex. The slightly raised distal expansion, hollowed above like a shovel, is irregularly semi-circular in shape, and has a continuous unevenly denticulated edge, without median notch; and the apex of the shaft of the baculum projects forwards as a process from its lower surface. The bone measures about 3 mm., and the width of the distal expansion is about half the length of the shaft. (Text-fig. 26, A, B.)

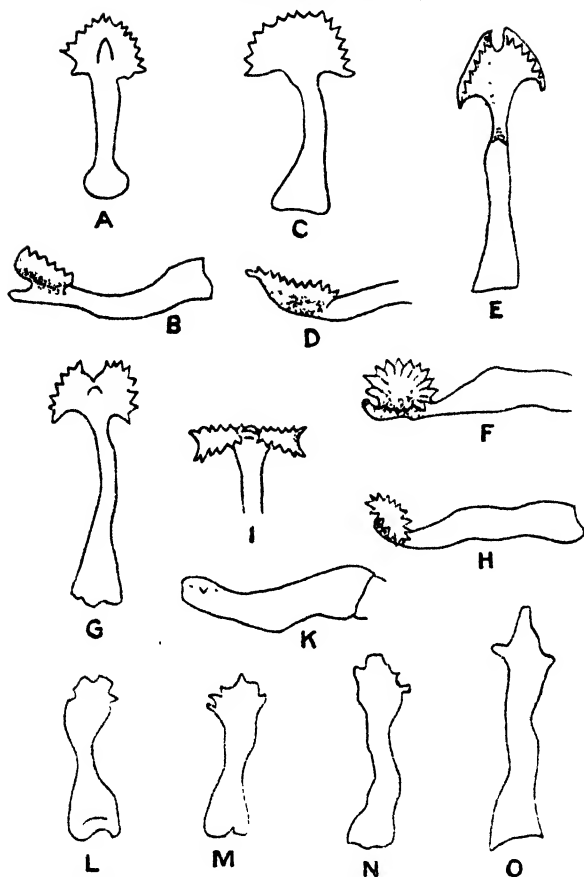
The baculum of a specimen of *C. leursi* from Jalisco, in Mexico, has the shaft very broad at the base, whence it gradually narrows to the expansion. Its upper and lower edges are nearly straight from the lateral view, but from the dorsal view the shaft is seen to bend distally slightly towards the right. The disc is relatively and actually much wider than in *C. mongolicus*, and its right side is produced more than the left; but its edge is continuous, without median notch and more regularly denticulated than in *C. mongolicus*. There is, moreover, no process representing the tip of the shaft on the under side of the disc. The bone measures 5 mm., and the width of the disc is almost equal to the length of the shaft. (Text-fig. 26, C, D.)

In two examples of *C. mexicanus*, one from the City of Mexico, the shaft differs from that of *C. mongolicus* and *leursi* in having its upper edge abruptly inclined downwards and distally towards the disc; and the disc itself differs in having a deep median notch in its margin and in being much more strongly bent upwards, so that its hollow is much deeper and more triangular in shape. As in *C. mongolicus*, the apex of the shaft is continued as a short process projecting from the lower surface of the disc in front a little beneath the notch. The bone measures about 5.5 mm. and the greatest width of the disc across its posterior angles is less than half the length of the shaft. (Text-fig. 26, E, F.)

In a specimen of *C. 13-lineatus* from Minnesota the shaft is intermediate in shape between that of *C. mexicanus* and of *C. leursi*; but the disc differs from that of the other species in having its edge broad and furnished with two rows of teeth. It is, moreover, very definitely divided into a right and left lamina by a wide and moderately deep median notch in front, and it is somewhat abruptly upturned. The tip of the shaft shows as a low, indistinctly defined rounded boss on the under side of the disc just below the notch. The bone measures 5 mm. and the width of the disc is about half the length of the shaft. (Text-fig. 26, G-H.)

- a. Edge of the apically widely notched disc broad and armed with two rows of teeth 13-lineatus.
- a'. Edge of the disc narrow and armed with a single row of teeth.
- b. Disc nearly vertically upturned, with a narrow median notch in front; upper surface of shaft distally geniculate..... .. mexicanus.
- b' Disc a little upturned, without median notch; shaft not distally geniculate above.

Text-figure 26.



- A. Baculum of *Citellus mongolicus*, from below.
 B. The same from the left side.
 C. Baculum of *C. leucurus*, from below.
 D. Apex of the same from the left side.
 E. Baculum of *C. mexicanus*, from above.
 F. The same from the left side.
 G. Baculum of *C. 13-lineatus*, from below.
 H. The same from the left side.
 I. Apex of the same from above.
 K. Baculum of *Cynomys ludovicianus*, from the left side.
 L. The same from above.
 M. The same of another specimen, from below.
 N. Baculum of *Marmota marmota*, from below.
 O. The same of another specimen.

- c. Disc comparatively small, its width about half the length of the shaft, the tip of the shaft projecting as a process beneath it *mongolicus.*
- c'. Disc very wide, its width almost equal to the length of the shaft, the apex of which forms no projection beneath it in front *leucis.*

In *Cynomys ludovicianus* the glans penis is short, its proximal two-thirds being stout and subcylindrical and its distal third forming a quite narrow terminal process sharply defined from the thicker portion. The orifice lies on the right side close to the base of the narrowed end. The baculum, measuring 4 mm. in length, lies in the narrowest portion and reaches its apex. It is broader at the base and tip than in the middle and is slightly asymmetrical. Its upper edge is very slightly concave, its lower edge mesially geniculate, the apex being irregularly denticulated. (Text-figs. 25, I; 26, K-M.)

In *Marmota marmota* the glans penis is shaped very much like that of *Cynomys*, but is relatively a little shorter. The orifice opens similarly on the right side at the base of the narrowed terminal process and the baculum, measuring only 7 mm., and lying in the narrowed piece is a slightly asymmetrical bone with expanded base and expanded irregularly denticulate apex. It is not quite alike in two specimens examined, and I am unable to affirm any character apart from size by which it may be distinguished from the baculum of *Cynomys*. (Text-figs. 25, K; 26, N, O.)

It may be recalled that Tullberg many years ago described the glans penis of *Marmota* [*Arctomys*] as very small and asymmetrical, with the opening on the right side behind the tip, which carries a small baculum. The male genitalia of *Cynomys* he described as like those of *Marmota*; but, what is more interesting still, he declared the male genitalia of *Tamias* to be also very similar to those of *Marmota*.

6. The Subfamilies of *Sciuridæ*.

For the following grouping of the genera of non-volant Squirrels, constituting the *Sciuridæ*, I take the glans penis and the baculum as supplying characters of primary value. It may be objected that these characters apply only to one sex; but I do not think it can be doubted that corresponding differences occur in the females and merely await discovery. The baculum has been examined either by Mr. Thomas or myself in all the principal genera, and the penis by Tullberg and myself in a considerable number of them. As subsidiary characters I have used the ears and feet, leaving alone cranial and dental characters, the study of which by Thomas, Forsyth Major, and many American authors has led to no very satisfactory result apart from the steady but unavoidable and convenient multiplication of genera and subgenera.

Subfamily SCIURINÆ.

Glans penis apically expanded, compressed and upturned, enveloped behind the upturned tip in soft swollen tissue. Baculum large, with compressed terminal blade hollowed on the right side, which carries inferiorly a short downwardly directed process.

Ears relatively long, more tubular at the base, with large angular antitragal flap.

Feet with fourth digit the longest; the plantar, carpal, and metatarsal pads normal and relatively simple.

Genera: *Sciurus*, with subgenus *Tenes** for *persicus*; all the American subgenera or genera, *Neosciurus*, *Parasciurus*, *Echinosciurus*, etc., except *Tamiasciurus*; ?*Rheithrosciurus*.

Distribution. Holarctic and Neotropical Regions and ? Borneo (*Rheithrosciurus*).

I feel compelled to include *Rheithrosciurus* provisionally in this group, pending confirmation or refutation of Thomas's statement that the baculum is like that of *Sciurus*. In other external characters supplied by the ears and feet it is certainly unlike other Oriental species and comes nearer to *Sciurus*. On the evidence at present available I should judge it to be a highly specialised member of the Sciurinae as above defined.

Subfamily TAMIASCIURINÆ.

Distinguishable from the Sciurinae, which it resembles in cranial and other external characters, by the structure of the penis, which is relatively long and slender and tolerably evenly attenuated from base to apex, and flexible throughout owing to the suppression of the baculum.

Genus *Tamiasciurus*.

Distribution. Nearctic Subregion.

The general resemblance between *Tamiasciurus* and the typical Sciurinae suggests that it is a specialised offshoot of that group. It is a very remarkable fact that the extreme differentiation of the penis does not appear to be correlated with other variations from the Sciurine type.

In the structure of the penis *Tamiasciurus* shows to a certain extent a convergent resemblance to the African genus *Heliosciurus* (see below, p. 238).

Subfamily FUNAMBULINÆ.

A highly diversified group of genera, with the glans penis exceedingly variable in size and structure and the baculum either

* Thomas, Ann. & Mag. N. Hist. (8) iii. p. 468 (1909).

relatively very large (*Funambulus*, *Tamiodes*), relatively small (*Ratufa*, *Protoxerus*), minute (*Funisciurus*, *Paraxerus*, *Ethosciurus*), or absent (*Heliosciurus*). It is, however, when present, always a simple bone without the spatulate expansion at the apex seen in the *Sciurinae*, without the accessory blade of the *Tomeutinae*, and without the compressed downturned lamina of the *Xerinae*. The ears are always relatively shorter and wider and less tubular at the base than in the *Sciurinae*, but are without the peculiarities of the ears of the *Xerinae* and altogether better developed.

Genera: *Funambulus*, *Tamiodes*, *Ratufa*, *Protoxerus*, *Ethosciurus*, *Funisciurus*, *Paraxerus*, *Heliosciurus*, and probably the other African genera admitted by Thomas, including possibly even *Myosciurus*.

Distribution. Oriental and Ethiopian Regions.

When the genera are better known, this group will perhaps be split up into several subfamilies. So far as my observations go, the genera fall into the following sections by the characters established in this and my previous paper:—

- a. *Tamiodes*, with a thick glans penis with terminal labiate orifice and a large baculum with its distal extremity bent upwards at a right angle to the rest of the shaft.
- β. *Funambulus*, with the glans terminally narrowed, the simple orifice on its right side, some distance behind the tip of the glans, and, the baculum large and gently curved upwards distally.
- γ. *Ratufa*, with the baculum relatively quite small, curved as in *Funambulus*, but stouter and bevelled below distally; (glans unknown); the feet in their pad development quite different from those of the other genera.
- δ. *Protoxerus*, with the glans possessing a median swollen area carrying the orifice, and an elongated narrower distal portion supported by a relatively small baculum not differing greatly from that of *Ratufa*, but with a button-like apex and a scalloped proximal end.
- ε. *Funisciurus*, *Paraxerus*, *Ethosciurus*. Glans with a marked median grooved or laminate swelling and a slender distal portion as in *Protoxerus*; but the distal portion flexible, laterally serrulate, and carrying a minute undifferentiated baculum close to the apex.
- ζ. *Heliosciurus*. Penis and glans exceedingly long, the glans with narrower, longer swelling, and exceedingly thin, long filiform distal portion without trace of baculum.

Of other genera that have been established, *Tamiscus*, recently dismembered from *Paraxerus*, probably falls into section ε. But whether *Epixerus* comes into δ or ε I am unable to surmise. Probably an examination of the glans penis and baculum will

settle the doubtful question as to the affinities of the genus with *Protoxerus* or *Funisciurus*. Of the genitalia of *Myosciurus*, I know nothing beyond Thomas's statement that the baculum is simple as in other African genera. The position of *Myrsilus* is also doubtful.

Subfamily CALLOSCIURINÆ.

Glans penis variable in shape and length according to the baculum; the orifice close to the tip on the right side. Baculum long and slender or short and stout, slightly or strongly upturned distally, and always provided with an accessory blade, movably jointed to the concavity of the upper surface.

Ears as in *Funambulinæ*.

Feet, where known, intermediate in structure between those of the more primitive types of the *Funambulinæ* (*Funambulus*) and the specialised genus *Ratufa*.

Genera: *Callosciurus*, *Menetes*, *Tomentes*, *Rhinosciurus*, *Lariscus*, *Dremomys*, *Tamiops*, *Naumosciurus*, and probably others.

Distribution. Oriental Region from India to China and Borneo.

This group may perhaps be regarded as a specialised offshoot from the *Funambulinæ*. The simplest type of baculum, e.g. that of *Callosciurus*, may be derived from that of *Funambulus* by the addition of the blade. But the subterminal position of the orifice is as in the *Sciurinae*.

Subfamily XERINÆ.

Glans penis, where known, with a strongly convex crested upper distal edge and a downwardly directed, rounded or truncated apex. Baculum with a stout, longer or shorter subcylindrical proximal portion, and a compressed downturned terminal blade with a median crest above and frequently a laterally expanded upper surface.

Ears more or less reduced, but with large fleshy antitragal thickening.

Feet with strong fossorial claws and the third digit the longest.

Fur scanty and harsh. An additional tuft of superciliary vibrissæ over the posterior corner of the eye.

Genera: *Atlantoxerus*, *Xerus*, *Euxerus*, *Geosciurus*.

Distribution. Africa from Morocco to Cape Colony.

The structure of the penis and baculum alone serves to negative the idea that this group of African Ground-Squirrels is closely akin to certain African arboreal Squirrels, an idea which prompted the proposal by Major of such names as *Protoxerus* and *Paraxerus* for two genera of the latter category. The *Xerinae*, indeed, are in addition distinguishable from the rest of the

African genera of the family by their ears, feet, fur, and the additional tuft of superciliary vibrissæ, and by the cranial characters pointed out by Thomas in his paper on African Squirrels.

Subfamily MARMOTINÆ.

Glans penis, at least in *Marmota* and *Cynomys*, very small, a diminutive copy indeed of that of *Funambulus* but with the point not upturned by the curvature of the baculum; also somewhat resembling that of *Funisciurus* and *Paraxerus*, except that the proximal thickening and the terminal narrowed piece are structurally simple and less sharply differentiated. Baculum also relatively very small, highly specialised with a symmetrical terminal, denticulated lamina in *Citellus*, but ending simply with a few irregularly placed denticles in *Marmota* and *Cynomys*.

Ears simplified, without tragal or antitragal thickenings, but with a hairy expansion of the anterior rim extending into the cavity beneath the supratragus.

Feet with fossorial claws and the third digit not shorter than the fourth.

Genera: *Marmota*, *Marmotops*, *Cynomys*, *Citellus* with many subgenera, ? *Tamias*, and *Eutamias*.

Distribution. Holarctic Region.

Although admitted as a subfamily in many text-books, this group was not granted that rank by some competent judges, e. g. Forsyth Major and Miller, on account of the closeness of its kinship with the true Squirrels. It appears, however, to be sufficiently well characterised to be admitted.

I have provisionally included *Tamias* and *Eutamias* mainly on the strength of Tullberg's statement that the genitalia are similar to those of *Marmota*, but also because *Tamias* and *Citellus* are alike in the presence of large cheek-pouches, a character in which they differ from all the typical Squirrels.

Nevertheless the feet of the only example of this group I have seen in a fresh state, namely a female of *Eutamias quadri-rittatus*, are not like those of *Citellus*, and hardly differ from those of the Squirrels. The ears, too, do not show the special features characteristic of those of *Citellus*, *Marmota*, and *Cynomys*, but are more like those of *Sciurus*. More extended observations on the two genera are required to determine their exact systematic status. Possibly they will prove to be worth ranking as a special subfamily—Tamiinæ.

7. The Flying Squirrels.

The Petauristidæ were classified by Thomas in 1908*. Setting aside *Petaurista*, he took the genus *Sciuropterus*, already shown by Heude and Forsyth Major to be composed of heterogeneous

* Ann. Mag. Nat. Hist. (8) i. pp. 1-6.

elements, and pointed out that it is divisible by the structure of the teeth into six genera:—*Sciuropterus*, type *russicus*, for the Palearctic species; *Trogopterus* for *xanthipes* from China; *Belomys*, type *pearsoni*, *Pteromyscus*, type *pulverulentus*, *Petaurillus*, type *hosei*, and *Ionys*, type *horsfieldi*, from various parts of the Oriental Region, each containing one or more species besides the type. Furthermore, he divided *Sciuropterus* into four subgenera: *Sciuropterus* itself; *Glaucomyys* for the North American *volans* and the Himalayan *fimbriatus**; *Hyllopetes*, containing many species ranging from Nepal to the Malay Islands, with *everettii* as the type; and *Petinomys*, ranging from Ceylon into South India and the Malay Islands, with *lugens* as type.

Owing to lack of material, I can contribute very little to what has been already established as to the affinities of the genera of this family. The outstanding result of my examination of the bacula is the complete severance of *Eoglaucomyys* from *Glaucomyys*. This suggests that further surprises may be in store for him who has the time and opportunity to carry on the work.

The penis and baculum are as variable in the Petauristidæ as in the Sciuridæ. The penis itself is only known to me in two genera, *Eoglaucomyys* and *Hyllopetes*, of which one specimen of each, preserved in alcohol, has been available.

In *Eoglaucomyys fimbriatus* the glans is stout and tolerably long, a little stouter just beyond the middle than at the base, and slightly upcurled but not appreciably narrowed at the end. On the left side above, just before the tip, there are three processes in a line, the first and third short and semiconical, the second or middle one much higher and roughly three-sided. Beyond these the apex of the glans forms a lamina hollowed on the left side, and beneath this there is a rounded area with a fleshy flap defined by a groove which passes backwards on to the right side, where the area in question is narrowed and runs backwards, being defined above and below by a groove. The orifice appears to be situated towards the posterior end of the upper groove, and from the orifice two more grooves run backwards to the proximal end of the glans. (Text-fig. 27, A-C.)

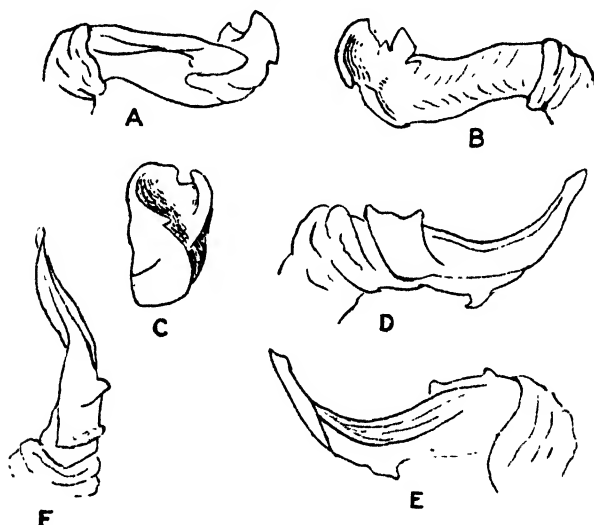
The baculum, measuring 7.5 mm., is exceedingly short and occupies only the distal half or less of the glans. It is furnished with several processes, and agrees tolerably closely in shape to the shape of the end of the glans. It is indeed the bony processes of the baculum, enveloped in soft tissue, which give shape to the end of the glans; but the rounded area of the glans below the distal hollow is wholly composed of soft tissue, no portion of the baculum entering it. The proximal end of the baculum forms a short, stout rod, shorter than the terminal toothed portion and emarginate below. Considering the former association,

* This species was subsequently separated from *Glaucomyys* as the type of the subgenus *Eoglaucomyys*.

suggested by their names, of *Eoglaucomy's* with the North American *Glaucomy's*, the differences between their bacula are very striking and suggest that the resemblances between the genera, which induced Thomas in his revision of the Petauristidæ to refer *fimbriatus* to *Glaucomy's*, are purely convergent. The differences between their bacula are apparently indeed greater than the differences between the bacula of any other two species. (Text-fig. 29, H-K.)

In *Hylopetes alboniger* the glans penis is very different from that of *Eoglaucomy's*. The distal half of the glans is narrowed and curved considerably towards the left and upwards at an

Text-figure 27.



A, B. Glans penis of *Eoglaucomy's fimbriatus*, from right and left sides.

C. Apex of the same from the front.

D, E, F. Glans penis of *Hylopetes alboniger* from right side, left side, and above.

angle of about 135° . On the left side of the upturned portion there is a crest running downwards from the apex and ending near the middle of the lower convex surface in a well-marked compressed point. Near the base of the glans on the upper surface there are two crests, one in front of the other and defining a kind of saddle-shaped area; these crests pass downwards on to the right side of the glans. I could not find the orifice of the organ of the specimen examined. (Text-fig. 27, D-F.)

The baculum, measuring 13 mm., is shaped distally like the distal portion of the glans, having the same upward and sinistral curva-

ture. There is a well-developed crest on its left side, passing from the apex down to the inferior tooth which is the termination of the crest. But although the baculum is long and extends throughout the length of the glans, it shows no trace of crests or processes behind the termination of the crest inferiorly. This baculum differs from that of *Eoglaucomyss* in its length, its simple apex, and the lateral inferior crest. (Text-fig. 28, C, D.)

Of this baculum I have seen two specimens, one taken from the spirit-preserved example from the Himalayas in the Zoological Society's collection, the other from an example from Mishmi in the British Museum.

The baculum of a specimen of *Hylopetes phayrei* from Burma, in the British Museum, measures 11 mm., and agrees very closely with that of *H. alboniger*, but is less markedly upcurled distally and is provided with a larger crest. (Text-fig. 28, E.)

Hylopetes, it may be recalled, was regarded by Thomas as a subgenus of *Sciuropterus*. Since the baculum of *Sc. russicus* does not appear to have been described, it is impossible to give an opinion as to the precise status of *Hylopetes*. But if, as appears to me probable, the baculum of *Sciuropterus russicus* resembles that of *Glaucomyss volans*, full generic value should, I think, be given to *Hylopetes*.

The baculum of an example of *Petinomys fuscocapillus* from Ceylon, in the British Museum, is a tolerably stout bone with a sinistral curvature like that of *Hylopetes*, the right side being convex, the left side concave, but it has no very marked upward curvature, the upper edge being slightly sinuous and the apex a little raised, almost as in *Hylopetes phayrei*. The apex, however, is broader than in *Hylopetes* and somewhat spatulate, the left margin of the shallow apical hollow being raised into an angular tooth behind. On the lower side of the bone there is a strong crest divided by a notch, about in the middle of the bone, into a short proximal and a long distal portion. The latter, which is angled behind, forms a sinuous curve towards the left, but does not ascend on to the left-hand side of the bone distally, as in *Hylopetes*, but terminates on the lower side of the expanded spatulate apex. The baculum measures 11 mm. (Text-fig. 28, F-H.)

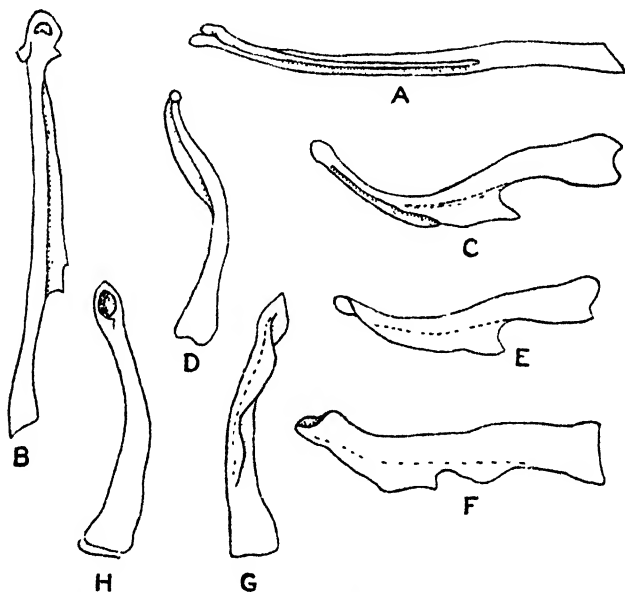
In view of the affiliation by Thomas of *Petinomys* with *Hylopetes* as subgenera of *Sciuropterus*, it is interesting to note the broad general resemblance, associated with marked differences, between their bacula.

The baculum of *Glaucomyss volans*, judging from two specimens in the British Museum, one of which is ticketed Virginia, is exceedingly long and slender, slightly sinuous in its proximal third, and inclined slightly upwards distally. The extreme apex is bifid, the lower process being rounded, the upper more pointed. On the left side there is a long crest running from the summit of the upper terminal process and ending abruptly behind the left side about one-third of the distance from the proximal end of

the bone. It lies over a well-marked groove, and there is a second shallower groove on the right side of the bone. The bone measures 12.5 mm. (Text-fig. 28, A, B.)

Despite its straightness and apical notch, this baculum is similar in type to that of *Hylopetes*, the crests on the left-hand side of the two corresponding closely. The crest in *Glaucomys* terminates on the left side of the bone instead of passing on to its lower surface as in *Hylopetes*. The surprising differences

Text-figure 28.



- A. Baculum of *Glaucomys volans*, from the left side.
- B. The same from below.
- C. Baculum of *Hylopetes alboniger*, from the left side.
- D. The same from below.
- E. Baculum of *H. phayrei*, from the left side.
- F. Baculum of *Petinomys fuscocapillus*, from the left side.
- G. The same from below.
- H. The same from above.

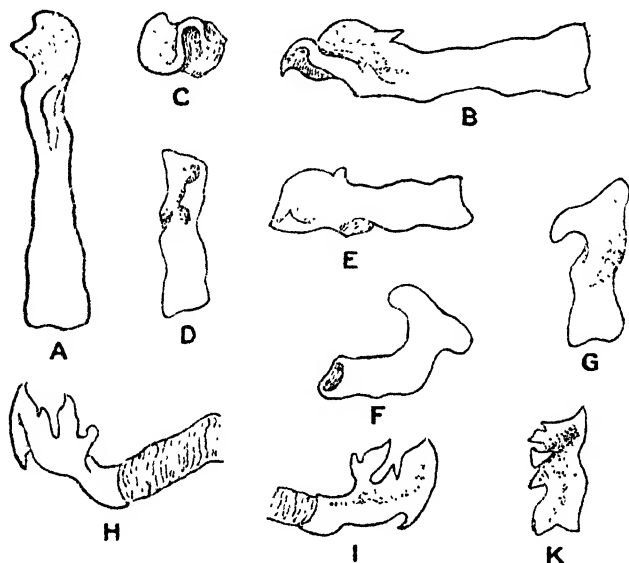
between the bacula of *Glaucomys* and *Eoglaucomys* have already been mentioned under the description of the latter genus.

The baculum of a specimen of *Belomys* (?) *trichotis* from Yin, Chindwin, in the British Museum, is hardly longer than that of *Eoglaucomys*, but is otherwise very different from it. The proximal portion consists of a stout subcylindrical "handle," sharply geniculated where it passes into the abruptly upturned distal portion, which ends in a wide lamina, shaped like a

hammer-head and lying obliquely and transversely, the shorter right-hand branch projecting farther forwards than the longer left-hand branch. This baculum is quite unlike that of any other species of the *Petauristidæ* examined. (Text-fig. 29, F, G.)

The baculum of an example of *Petaurista philippensis* from Kanara, in the British Museum, is a long, stout bone, gradually

Text-figure 29.



- A. Baculum of *Petaurista philippensis*, from above.
- B. The same from the left side.
- C. Apex of the same from the front.
- D. Baculum of *Petaurista* sp. ? from above.
- E. The same from the left side.
- F. Baculum of *Belomys trichotis*, obliquely from behind.
- G. The same from above.
- H. Baculum of *Foglaucomys ambriatus*, from the left side.
- I. The same from the right side.
- K. The same from above.

narrowing from the base to the slightly expanded and upturned distal end, which, when viewed from the front, is seen to be shaped rather like the widened spout of a jug, the lower rim of the spout being evenly rounded. From the side this terminal lamina has a rounded upper border, a rather deeply emarginate and thickened distal border, and a nearly straight, obliquely ascending, thickened posterior border ending inferiorly in a small

tooth. Just below the hollow on the left side there is a small crest ending above in another small tooth. The bone measures 20 mm. in length. (Text-fig. 29, A-C.)

The baculum of another but unidentified and unlocalised species of *Petaurista* in the British Museum differs in some well-marked characters from that of *P. philippensis*. It measures only 8 mm. owing to the shortness of the proximal portion, which does not exceed the distal portion in length. The latter has its hollowed surface looking more to the left, the upper or right-hand rim being more, and the lower or left-hand rim less elevated than in *P. philippensis*, and its distal rim is not curved over and spout-like. If the ossification of the baculum proceeds backwards from the distal to the proximal end, it is possible that the difference in the length of this bone in *P. philippensis* and the unidentified species is a matter of age. (Text-fig. 29, D, E).

The following table shows how the genera examined may be distinguished by their bacula:--

- | | |
|--|----------------------|
| a. Baculum with crest running from the comparatively small and simple apex backwards along the left or under side of the bone. | |
| b. Baculum nearly straight, comparatively long and slender; apex bilobed, crest confined to left side | <i>Glaucomya</i> . |
| b'. Baculum shorter, stouter, more curved; apex undivided, crest wholly or partially ventral. | |
| c. A single crest curving distally up on to the left side of the bone to the apex, which is simple, not spatulate . . . | <i>Hypopetes</i> . |
| c'. A supplementary crest behind the main crest, which is entirely ventral; apex spatulate | <i>Petinomys</i> . |
| a'. Baculum without lateral or ventral crest, with expanded complex apex. | |
| d. Distal end of baculum abruptly upturned and ending in a two-headed or hammer-shaped lamina | <i>Belomys</i> . |
| d'. Distal end of baculum not abruptly upturned, the apex expanded, more or less hollowed, and complicated with accessory processes. | |
| e. Apex of baculum hollowed, irregularly spatulate, with small accessory processes | <i>Petaurista</i> . |
| e'. Apex of baculum armed with uprising spiniform processes on the left side | <i>Eoglaucomya</i> . |

18. On the Mammals obtained in Darfur by the Lynes-Lowe Expedition. By OLDFIELD THOMAS, F.R.S., F.Z.S., and MARTIN A. C. HINTON, F.Z.S.

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Thanks to the generosity and public spirit of the two explorers, the British Museum has received as a donation the whole of the fine collection of Mammals made by Rear-Admiral Hubert Lynes and Mr. Willoughby P. Lowe during their recent expedition to Darfur.

The expedition took place during the whole of 1921 and the early part of last year, and a complete survey of the country was made, equally of the comparatively flat desert region round El Fasher, the capital of Darfur, the still more desert area northward to the bare and unproductive Jebel Maidob, the zoologically unknown dominating mountain Jebel Marra, running up to a height of 10,000', and, finally, of the lower region of Wadi Aribu, in the south-western part of Darfur, where the drainage is towards Lake Chad.

No mammal collection had ever been made in this area, so that the present fine series (which numbers upwards of 800 specimens) adds very greatly to the material available for the study of African Mammalia, and we have reason to be most grateful to the donors for the generosity and patriotism which have resulted in this notable accession to the Museum—the largest single collection that the latter has ever received.

On the whole, the species contained in the collection are most nearly related, as is natural, to those of Kordofan and other parts of the Egyptian Sudan, and are generally different from those of the more humid Bahr-el-Ghazal.

So far as the mammals are concerned, Darfur would seem to be just on the southern boundary of the northern desert fauna, the collection containing quite a number of forms which are either the most southern records of northern species (*Taculus jaculus*, *Dipodillus campestris* group, etc.) or the most northern records of southern ones (*Stenomys*, &c.).

The great mountain Jebel Marra, isolated as it is from other high ground, has naturally a number of interesting forms peculiar to it and different from those of the plains. Thus there is a mountain species of Striped Mouse (*Lemniscomys*) found on it, which we have named in honour of Admiral Lynes, and a Gerbil (*Dipodillus lowei*), whose nearest ally is found in Algiers.

In all, the collection proves to consist of 62 species, of which we have had occasion to describe 19 as new, either as species or subspecies.

A few mammals were obtained by Admiral Lynes on a previous visit to the country, and these have been here incorporated. Their numbers run from 1 to 24, while those of the main collection start at 400.

1. *ERYTHROCEBUS PYRRHONOTUS* Hempr. & Ehr.

♂. 648. ♀. 672. Foot-hills, S. Jebel Marra. 4000'.

Practically the first satisfactory examples of this species to reach the Museum.

2. *CERCOPITHECUS TANTALUS MARRENSIS*, subsp. n.

♂. 631. Foot-hills, S. Jebel Marra. 4000'.

♀. 626, juv. S.W. Jebel Marra. 5000'.

A very brightly coloured subspecies.

Face and chin black. White brow-line well defined, with an anterior edging of black hairs. Whiskers yellowish white, directed backwards and upwards, completely concealing ears. A sharply defined black streak from outer canthus of eye to neighbourhood of ear, separated from the crown-patch by a narrow tract of white whisker-hairs. Predominant hue of upper parts (crown of head, back to rump, and flanks) bright buff or golden, darkened on crown of head and rump by black hair-tips and to some extent by the hair-bases of slate-grey, which are darkest on the crown of the head. The golden tint is especially bright and clear upon the withers and flanks. Under surface of body, with inner surfaces of limbs, well-haired, pure white and rather sharply contrasted with flanks. Outer surfaces of arms and hands from shoulders, and of the legs and feet, from the thighs, of a general light grey colour of cold tone, produced by a mixture of pale slate-grey and dirty white, without any trace of buff. A tuft of white hair on each side of the root of the tail above. Upper surface of tail, in its proximal two-thirds, like the rump; its lower surface in the same region white, becoming yellower distally. Distal third of tail, above and below, dull yellow.

Dimensions of the type (measured in the flesh):—

Head and body 830 mm.; tail 1140; hind foot 145; ear 32.

Skull: extreme length 118.6; condylo-basal length 88; zygomatic breadth 68.2; external orbital width 62.6; postorbital constriction 44; width of brain-case 56.5; canine to m^3 34.2; p^3-m^3 25.4.

Hab. Foot-hills of Jebel Marra.

Type. Adult male. B.M. No. 23.1.1.1. Original No. 631. Collected April 1, 1921.

This is a very well-marked subspecies of *C. tantalus*, a species known to range from Nigeria and the West Coast eastwards to the shores of Lake Albert. *C. toldti* Wettstein, described from Kadugli, S. Kordofan, on the basis of rather unsatisfactory material, appears to be a member of the "*callitrichus*" or *sabæus* group.

3. *PAPIO ANUBIS* F. Cuv.

♂. 8. Jebel Marra. 7000'.

Shot and presented to Admiral Lynes by Mr. Cecil McConnel.

4. *GALAGO SENNAARIENSIS* Less.

♂. 781, 804. ♀. 783. Kulme, Wadi Aribo. 3300'.

5. *EIDOLON HELVUM* Kerr.

No specimens of this bat were obtained. But a stem of a small tree, which Mr. A. S. Brown has identified as being either an *Odina* or a *Sclerocarya*, completely gnawed through, was found on Jebel Marra and brought home by the collectors as evidence of the existence of some large rodent upon the mountain. The tooth-marks, however, are very different from those of any rodent.

In 1920 Mr. R. H. Bunting, of the Agricultural Department of the Gold Coast, sent us some specimens of *Araucaria*, from a grove at Aburi, which had been seriously damaged by large bats in a time of drought. With the timber came some of the bats, caught in the act, and they proved to be *Eidolon helvum*. The bitten wood from Jebel Marra is exactly like that from Aburi. and may be regarded, perhaps, as good evidence of the presence of this bat in certain seasons upon the mountain.

6. *HIPPOSIDEROS CAFFER* Sund.

♂. 887. ♀. 885, 886. Kulme, Wadi Aribo, 3300'.

♂. 939. ♀. 954. Zalingei. 3300'.

1174. 170 miles E. of El Fasher.

Forearm 48-49 mm.

7. *ASELLIA TRIDENS* Geoff.

♂. 6, 17, 18. ♀. 5, 19, 20, 24. Um Esheishat Well, 104 miles E. of El Fasher. 2200'.

These specimens were collected by Admiral Lynes during his preliminary visit to Darfur. Two of them were obtained on February 2, 1920, the others on May 13 following; all are in the brilliant red phase.

8. *PIPISTRELLUS MARRENSIS*, sp. n.

♂. 633, 653, 656. Foot-hills of S. Jebel Marra. 4000'.

Essentially as in *P. deserti* Thos., but of smaller size and darker colour.

Colour comparatively dark and rich, much like that of Egyptian specimens of *P. kuhli*, the general hue of the upper parts being near "Dresden brown" of Ridgway. Ears noticeably darker than back. Wings dark brown, with usual whitish edgings; inter-femoral paler. Tragus shorter and broader than in *deserti*, with

broadly rounded tip and parallel borders; the inner border the longer. Forearm not exceeding 28 mm. (29·8 in *deserti*).

Apart from its slightly smaller size, the skull agrees with that of *P. deserti*. The outer upper incisor and the small upper premolar p^2 appear to be a little more reduced than in *deserti*, but the available material shows a rather wide range of variation in these respects. In the type-skull i^2 is both absolutely and relatively much smaller than in the only known skull of *deserti*; and the point of the tooth does not rise above the cingulum of i^1 . The small premolar is also greatly reduced, and so crowded between the canine and p^1 that it is not easy to detect. But in the fragments, all that is left of the two other skulls from Jebel Marra, the teeth in question, though rather smaller than in *deserti*, are considerably larger than in the type.

Dimensions of the type:—

Head and body 37 mm.; tail 21; hind foot 5·5; ear 12. Forearm 26·5; third finger 46 (m.c. 24·5; phalanges 8·7—7·5—5·5); lower leg and hind foot (c.u.) 14·5.

Skull: greatest length 11·2; median length above 9·6; median length below 8·1; interorbital breadth 4·3; intertemporal breadth 3·4; breadth of brain-case 6·7; canine to m^3 3·8.

Hab. Foot-hills, S. Jebel Marra; altitude 4000'.

Type. Adult male. B.M. No. 23.1.1.15. Original No. 633. Collected April 3, 1921.

This interesting little bat is, no doubt, closely related to *P. deserti*, described from Tripoli. Its smaller size, darker colour, shorter tragus, and possibly more reduced dentition seem to warrant its receiving distinct specific rather than subspecific rank. The individual variation noticed in the dentition is of some interest in a group in which, normally, even minute dental characters are surprisingly constant.

Both *marrensis* and *deserti* are apparently closely allied to *P. kuhli*; and we can see no good reason for placing them in the genus *Scotozous* (cf. Miller, *Fam. & Gen. Bats*, p. 206, 1907).

9. SCOTOPHILUS NIGRITA Schreb.

♂. 401. 60 miles W. of El Obeid.

♂. 639. ♀. 660, 662. Foot-hills, S. Jebel Marra. 4000'.

♀. 734, 735, 738, 743, 744, 745, 746, 748, 749. Zalingei. 2800'.

At Zalingei: "Very common around swampy ground" in May 1921. In a note dated Oct. 27, Mr. Lowe says "I believe all these bats are migratory, as I have not seen any since the last obtained" (Zalingei, May 31).

10. SCOTEINUS SCHLIEFFENI Pet.

♂. 411. 70 miles W. of Nahud, Kordofan.

♂. 1187, 1188. ♀. 1186. 35 miles E. of Nahud.

♂. 1197. 50 miles W. of El Obeid.

11. *TAPHOZOUS MAURITIANUS* Geoff.

♂. 794. Kulme, Wadi Aribo. 3300'.

12. *NYCTINOMUS TONGAENSIS* Wettst.

♀. 1171. 125 miles E. of El Fasher.

Forearm 49 mm.

We are agreed that, on the whole, it would be advisable to separate generically the species of this group with 4 lower incisors—*Nyctinomus* (genotype, *egyptiacus*)—from those with 6—*Tadarida* (type, *teniotis*). No species seem doubtful as to their allocation in one or other of the genera, and the separation will clearly be a convenience. And at the same time it will elude the disputed question as to whether *Tadarida* or *Nyctinomus* is the earlier name for the combined genus.

13. *ATELERIX ALBIVENTRIS* Wagn.

♂. 1159, 1165. Um Kedada.

Skull only: 1153. 32 miles E. of El Fasher.

14. *CROCIDURA DARFUREA*, sp. n.

♂. 740, 750, 751, 754, 755, 877, 878, 909, 929, 931, 937, 943, 945, 946, 950, 955. ♀. 733, 739, 758, 876, 893, 934, 941, 944. Zalingei, Darfur. 2800-3300'.

♂. 827, juv. ♀. 833, 894, 919. Unsexed. 892, 907, 926. Kulme, Wadi Aribo. 3300'.

A large species resembling *C. sururre* in colour, but with much shorter tail.

Size large (hind foot about 18 mm.; condylo-incisive length of skull in adult male about 29). Tail short, about half the length of the head and body. General colour of dorsal surface pale, in lighter specimens near "citric-diab" of Ridgway, in darker ones approaching "hair-brown." Underparts lighter and greyer, with a decided wash of silver in fresh full fur. No sharp flank-line. Flank-gland on each side marked by a small patch of white hairs. Upper surfaces of hands, feet, and tail essentially concolorous with back; but tail often a little darker and sometimes dusky, its lower and upper surfaces similar.

Skull essentially as in *nyansæ* and *sururre*.

Dimensions of the type (measured in the flesh):—

Head and body 122 mm.; tail 65; hind foot 18; ear 13.

Skull-measurements of type (with those of an adult female in parentheses): condylo-incisive length 29.4 (27.3); greatest breadth 12.2 (11.4); least interorbital breadth 4.9 (5); upper tooth-row 13 (12.4).

Hab. Darfur.

Type. Adult male. B.M. No. 23.1.1.40. Original No. 755. Collected June 4, 1921, at Zalingei, Darfur. Altitude 2800'.

This Shrew is the local representative of *C. nyansæ* and *C. surura*. Resembling the latter in colour, it is distinguished from both by its relatively shorter tail. In the type of *surura*, the tail measures only 64 mm. with a head and body measurement of 111; but the material in the Museum indicates that *surura* normally has a tail of 75 or 80 mm., which is therefore considerably more than half the length of the head and body.

In this species there seems to be a well-marked sexual difference of size—female skulls being usually less, and males more than 28 mm. in condylo-incisive length.

15. *CROCIDURA HINDEI* MARRENSIS, subsp. n.

♂. 545. Wadi Kongei, East Central Jebel Marra. 6200'.

♀. 544. Wadi Barei, N.W. Jebel Marra. 6000'.

Closely resembling *C. h. diana* Dollman, but darker in colour and with a longer tail.

Size slightly smaller than in *diana*, but tail considerably longer (58 mm. instead of 48). Colour of upper parts darker, near the "snuff-brown" of Ridgway. Under parts greyish white. Flank-lines of demarcation regular, though not sharply defined. Hands and feet yellowish white above. Tail dark brown above, paler below.

Skull and teeth nearly as in *diana*; tooth-row a little shorter. The unicuspid teeth above without the peculiar narrowing and elongation of their crowns seen in *diana*.

Dimensions of the type (measured in the flesh):—

Head and body 74 mm.; tail 57; hind foot 12.5; ear 13.

Skull (posterior part broken): condylo-incisive length probably about 23; breadth of brain-case 9.5; least interorbital width 4.1; tooth-row 9.3.

Hab. Jebel Marra, at about 6000'.

Type. Adult male. B.M. No. 23.1.1.57. Original No. 545. Collected Feb. 27, 1921, at Wadi Kongei, East Central Jebel Marra.

C. h. diana, described from Lake Chad, is apparently the nearest ally of this Shrew. The darker colour, longer tail, and more normal dentition of *marrensis* force us, however, to treat it as a distinct subspecies.

16. *CROCIDURA ARIDULA*, sp. n.

♂. 846, 861, 928. ♀. 872. Kulme, Wadi Aribo. 3300'.

A grey Shrew resembling *C. butleri* Thos., but with a longer and unswollen tail.

Size medium. Tail normal, more than half the length of the head and body.

Colour of upper parts cold-grey, near the "deep greyish olive" of Ridgway. Under parts white, in sharp contrast with upper

parts along flanks. Hands and feet white above. Tail above concolorous with back, white below.

Skull essentially as in *butleri*.

Dimensions of type (measured in the flesh):—

Head and body 88 mm.; tail 43; hind foot 14; ear 12.

Skull: condylo-incisive length 23·3; breadth of brain-case 9·8; least interorbital width 4·2; tooth-row 9·8.

Hab. as above.

Type. Adult male. B.M. No. 23. 1. 1. 61. Original No. 928. Collected Sept. 21, 1921, at Kulme, Wadi Aribo. 3300'.

This species is sufficiently distinguished from *C. butleri* by its normal tail and somewhat colder colour.

17. *CROCIDURA MARITA*, sp. n.

♀. 673. S.E. Downs, Jebel Marra. 8650'.

A very small Shrew, related to *nana* and *religiosa*. Fur moderately long, hair of back measuring 3–4 mm. in length.

Colour of dorsal surface dark olivaceous grey; underparts greyish white; without any hard flank-line of demarcation. Hands and feet whitish. Tail indistinctly bicolor, dusky above, whitish below.

Skull flattened. Second and third unicusps about equal in size.

Dimensions (measured in the flesh):—

Head and body 56·5 mm.; tail 38; hind foot 10·5; ear 7·5.

Skull: condylo-incisive length 16·6; breadth of brain-case 7·5; least interorbital breadth 3·4; tooth-row 7·3.

Hab. as above.

Type. Adult female. B.M. No. 23. 1. 1. 63. Original No. 673. Collected April 21, 1921. S.E. Downs, Jebel Marra, altitude 8650'.

18. *FELIS OCREATA* Gmel.

♂. 450. El Fasher.

♂. 1062. 35 miles N. of El Fasher.

♀. 655. Foot-hills, S. Jebel Marra. 4000'.

"Lives in company with Fennec Fox. Said to be rare and local, living in colonies like rabbits."

19. *FELIS SERVAL* Schr.

♀. 855. Kulme, Wadi Aribo. 3300'.

"Native name Git."

20. *HERPESTES SANGUINEUS* Rüpp.

♂. 1141. El Fasher.

♂. 1061. 35 miles N. of El Fasher.

♂. 607, 611. ♀. 610, 974, 1019. Jebel Marra. 7100'–8000'.

♀. 758, 759, 762. Kulme, Wadi Aribo. 3300'.

Of this strongly-marked species the Museum previously possessed only a single specimen, which was also obtained by Admiral Lynes in this same region. It was originally described from Kordofan.

21. *HYÆNA HYÆNA* Linn.

♂. 412. 100 miles W. of Nahud.

♂. 641. Foot-hills, S. Jebel Marra. 4500'.

♀. 874 (skull only). Kulme, Wadi Aribo. 3300'.

"Does not appear to be found over 5000'."

22. *CROCUTA CROCOTTA* Erxl.

♂. 911. Kulme, Wadi Aribo. 3300'.

"This is the common species found here. Very destructive to sheep, goats, and donkeys. This individual stole three sheep out of our servants' huts."

23. *CANIS ANTHUS SUDANICUS* Thos.

♂. 426. 16 miles E. of El Fasher, Darfur. Jan. 29, 1921.

♂. 596, 597. Central Jebel Marra. 10,000'. March 10, 1921.

"Very common, and noisy at night. Usually seen in pairs."

♂. 683. S.E. Downs, Jebel Marra. 8000'. April 25, 1921.

"Very abundant on Downs."

♂. 935 (skull only). Jebel Marra. 9500'. "Feeds on insects which it obtains by scratching in the grass-roots. Stomach contained a large amount of vegetable matter, no doubt swallowed in the process."

♀. 1001. Jebel Marra. Dec. 6, 1921.

♀. 1015. Niurinya, Jebel Marra. 7000'. Dec. 29, 1921.

24. *VULPES PALLIDA* Rüpp.

♂. 829, 857. ♀. 858, and male skulls 914, 923. Kulme, Wadi Aribo. 3300'.

♂. 971. S.E. Jebel Marra. 8000'.

"Native name [at Wadi Aribo] Doctorri."

"Found in large colonies [at Jebel Marra]."

25. *ICTONYX STRIATUS SUDANICUS*, subsp. n.

♂. 666. Foot-hills of Jebel Marra, 4000'. April 16. B.M. No. 23. 1. 1. 95. *Type*.

An even lighter-coloured form than *intermedius*, with which it shares the narrowing of the black hairs of the nape and fore-back, and the breaking of the supraorbital black bar. Size decidedly larger than in *intermedius*, but only one specimen of each available for comparison. Fur long, loose, and shaggy.

Frontal white spots of medium size, the bar separating it from the temporal one on each side considerably broken by white hairs. Black lines of nape very narrow, much overlaid by the white hairs. Posterior black lines also at a minimum, the median one on the loins scarcely more than an inch broad, and its intensity much reduced by the long overhanging white hairs, the lines throughout less developed and sharply defined than in any other form. Chin and interramia largely intermixed with white hairs, a few only being present in *intermedius* and none in other forms. Black of under surface considerably narrowed in the ventral region, the white of the flank-bands encroaching on the belly on each side, while all across the latter there is an admixture of white with the black hairs. Tail with the basal portions of the hairs black as usual.

Skull fairly large, decidedly larger than in the type of *intermedius*, but smaller than in *shoa*.

Dimensions of the type (measured in the flesh):—

Head and body 355 mm.; tail 255 (not quite perfect); hind foot 58; ear 24.

Skull: greatest length (median) 68·5; condylo-basal length 66·5; zygomatic breadth 38·7; interorbital breadth 18; intertemporal breadth 16·3; mastoid breadth 33·7; palatal length 32·4; maxillary tooth-series 20; *p*' on outer edge 6·5.

Hab. and *Type* as above.

A form with the white markings at a maximum, in correlation with the desert characteristics of its habitat. *I. erythraea* is smaller, *shoa* larger and very dark-coloured, and *intermedius* somewhat similar in colour, but with much smaller skull and the usual wholly black underside.

26. *EUXERUS CHADENSIS* THOS.

♂. 436. El Fasher.

♀. 460. 35 miles S.W. of El Fasher.

♀. 1114. Jebel Maidob.

This desert Ground-Squirrel ranges along a strip at about 14° N. lat. for a considerable distance, as Capt. Buchanan obtained it at Zinder, French Nigeria; the typical series came from Lake Chad, and the present region is again much to the east of that lake. It is of very pale colour, and comparatively small (skull 58–61 mm.), though still much larger than the little *E. agadius* of the Air region (51·5 mm.).

27. *EUXERUS ERYTHROPUS LIMITANEUS*, subsp. n.

♀. 722. Zalingei, mouth of Wadi Aribo. 2800'.

♂. 803. ♀. 837, 854. Kulme, Wadi Aribo. 3300'.

♂. 657. Foot-hills of Jebel Marra. 4000'.

♀. 609. Central Jebel Marra. 7200'.

♂. 1. Dilling, Nuba Land. 2300'.

Larger than *chadensis* and *leucoumbrinus*. Colour about as in the latter.

Upper surface of body very much as in *leucoumbrinus*, that is to say near "saya-brown," decidedly darker than in *chadensis*. Light lateral line sharply defined white. Dull lateral line darker than the back.

Skull decidedly larger than in *chadensis* and *leucoumbrinus*, the total length of the skull about 61–63 mm.

Dimensions of the type (measured in the flesh):—

Head and body 270 mm.; tail 246; hind foot 65; ear 17.

Skull: greatest length 62; condylo-incisive length 58.5; zygomatic breadth 33.5; nasals 19; palatilar length 31.7; cheek-teeth exclusive of p^3 12; lower cheek-teeth 13.

Hab. Region of Wadi Aribu, extending eastward to Jebel Marra. Type from Zalingei.

Type. Adult female. B.M. No. 23.1.1.99. Original number 722. Collected 20 May, 1921.

Distinguished both from *leucoumbrinus** and *chadensis* by its larger size, and from *chadensis* by its darker colour, though the Jebel Marra specimens are a little paler than those from the Wadi Aribu.

28. *HELIOSCIURUS BONGENSIS* CANASTER, subsp. n.

♂. 671, 705. ♀. 663, 706. Foot-hills of Jebel Marra. 4000'.

A paler and greyer form of the *H. bongensis* of the Bahr-el-Ghazal.

Size as in *bongensis*. Dorsal colour as in that animal or inconspicuously paler. But sides, forearms, hips, and backs of legs far paler, whitish or greyish white. Under surface quite white to the bases of the hairs, a patch of buffy on each side of tarsus. Top of muzzle greyish white, much paler than the crown. White supra- and infra-orbital lines well marked; ears prominently whitish. Upper surface of hands and feet greyish white. Tail similarly ringed to that of *bongensis*, but paler throughout.

Skull about as in *bongensis*, equally smaller than that of *multicolor*. Nasals rather longer.

Dimensions of the type (measured in the flesh):—

Head and body 178 mm.; tail 217; hind foot 44; ear 15.

Skull: greatest length 44; condylo-incisive length 38.7; zygomatic breadth 26; nasals 14×6.8 ; interorbital breadth 13; maxillary tooth-row 8.8.

* With regard to *leucoumbrinus*, that species was founded by Rüppell in so vague and general a manner that it needs pinning down to some particular form, as it may have included quite a number of distinct races. There is in the British Museum one of his original specimens, purchased of the Senckenburg Museum (B.M. No. 79 b), and this we propose to select as a lectotype. It is of a pale cinnamon-brown colour, and corresponds in size with specimens having a skull-length of about 58 mm., its lower cheek-teeth 12 mm. It was received as from "Abyssinia," but how far this is trustworthy we are not in a position to state.

Hab. as above.

Type. Adult male. B.M. No. 23.1.1.107. Original number 705. Collected 8 May, 1921.

This Squirrel is a whitened desert representative of the Bahr-el-Ghazal *H. bongensis* Heuglin, a species distinguished from the better-known and widely distributed *H. multicolor* by its decidedly smaller size.

29. GRAPHIURUS OROBINUS Wagn.

♂. 963, 965. W. of Jebel Marra. 4000'.

♂. 771. ♀. 809, 918, 922. Kulme, Wadi Aribo. 3300'.

♀. 882, 930. Zalingei. 2800'.

Type-locality, Sennaar.

30. TATERA ROBUSTA Cr.

♂. 462, 463, 464, 466, 467, 499, 1068, 1086, 1128. ♀. 424, 443, 447, 456, 457, 458, 459, 460, 461, 465, 470, 480, 481, 482, 483, 484, 485, 490, 494, 495, 1144, 1152, 1154, 1155, 1173, 1175. El Fasher and neighbourhood.

♂. 1185. Nahud, Kordofan.

♂. 1193. ♀. 402, 1194, 1208. El Obeid.

♂. 1112. ♀. 1087, 1088, 1089. Jebel Maidob. 2750'.

♀. 1038. Tina Wells.

31. TATERA BENVENUTA Hint. & Kersh.

♂. 784, 807, 832, 836. ♀. 729, 801, 873. Kulme, Wadi Aribo. 3300'.

♂. 549. ♀. 548, 550. Wadi Kongei. 6200'.

♂. 529. ♀. 508, 523, 531, 585, 586, 649, 658, 700. Jebel Marra. 4000'–7900'.

TATERILLUS.

The genus *Taterillus* is represented by nearly 70 specimens, covering the whole area explored, except the upper part of Jebel Marra, where its place is taken by the special local form of *Dipodillus* described below.

In the district round El Fasher, two forms are found—the large bright-coloured *T. rufus*, with its naked whitish soles, and also a smaller species.

The other members of *Taterillus* in the collection all have the hair-band on the soles, and are related to *T. butleri* of Bahr-el-Ghazal, which seems to extend northwards into Kordofan, and we confess we do not see any reason to distinguish from it either *T. kadugliensis* or *Taterina lorentzi* of Wettstein. The distinction of *Taterina* from *Taterillus* as a genus is based on a character—

the presence of an extra cusp in m_1^* —which is far from constant, and many specimens of *Taterillus* have a rudimentary cusp in the same position. Major Graham has sent examples of *Taterillus* from S. Kordofan, which we may take as representing both *kadugliensis* and *lorentzi*, and these quite agree with the type of *butleri* from Bahr-el-Ghazal.

32. *TATERILLUS CLIVOSUS*, sp. n.

♂. 509, 516, 522, 525, 539, 645, 707. ♀. 519, 520, 521, 524, 647, 698, 699, 708, 1032. Jebel Marra. 4000'-5500'.

♂. 770, 830, 847, 860. ♀. 820, 848, 850, 862, 864, 865, 869. Kulme, Wadi Aribo. 3300'.

♀. 726. Zalingei. 2800'.

♂. 473. 35 miles W.S.W. of El Fasher.

♀. 1102, 1106. Jebel Maidob.

Like *T. butleri*, but with longer and rather more bushy tail.

Size about as in *butleri*, or a little larger. General colour buffy brown, a little lighter than in *butleri*, but decidedly darker than in the plains form to be described below. Face without special white markings. Ears of medium size, buffy brown, scarcely different from the back. Hands and feet white, soles blackish, generally with well-marked and often with very broad hair-bands. Tail decidedly larger than in *butleri*, and more heavily pencilled, its terminal two-fifths with blackish hairs upwards of 13 mm. in length, its upper surface brown, its lower buffy whitish. The type has a white tail-tip, but this is evidently abnormal.

Skull without special peculiarities, about 35-37 mm. in length.

Dimensions of type (measured in the flesh):—

Head and body 126 mm.; tail 182; hind foot 33; ear 20.

Skull: greatest length 37.5; condylar-incisive length 34; posterior palatine foramina 4.2; bulla 10; upper molar series 5.4.

Hab. Slopes of Jebel Marra below about 6000', and region of Wadi Aribo. Type from Jebel Marra, south, 5300'.

Type. Adult female. B.M. No. 23.1.1.127. Original number 698. Collected May 5, 1921.

* We are quite agreed that in systematic work it is, at least for the present and for a long time to come, better to use the conventional notation of m^1 , m^2 , m^3 for the three cheek-teeth of Muridae, rather than any notation which attempts to indicate their real homologies as compared with the cheek-teeth of other rodents. Mr. Kellogg has recently, in a paper dealing with certain Californian Voles (Univ. Calif. Publ. Zool. xxi. p. 245, 1922), described and figured the anterior tooth as the last premolar (p^4), the second tooth therefore as m^1 , and the third m^2 , a method which is liable, in systematic work, to give rise to a good deal of confusion. All the more that his revised nomenclature is by no means acceptable to other writers, as will be seen from a paper by Hinton (Ann. & Mag. N. H. (9) xi. p. 162, 1923), who reviews the whole question, and has reason to confirm the view that the anterior tooth is a milk-premolar (mp^4) and not a permanent one, a conclusion which Thomas also thinks may be the true one.

But in either case the conventional notation m^1 , m^2 , m^3 would seem to be the best for current systematic work.

This Gerbil, which is found in a more elevated region than *T. butleri*, resembles that species in its general colour, but differs by its longer and more bushy tail.

The determination of the last three specimens in the list is a little doubtful, but they may be provisionally assigned to the present form.

33. *TATERILLUS PERLUTEUS*, sp. n.

♂. 417. ♀. 416, 418, 419, 1160, 1161, 1178. Um Kedada, 100 miles E. of El Fasher. 2400'.

♀. 444, 446, 491, 492, 501, 1069, 1151, 1180. Neighbourhood of El Fasher.

♀. 1084, 1122, 1123. Tagbo Hills, 95 miles N.E. of El Fasher.

A smaller species of vivid buffy colour.

Size decidedly less than in *butleri* and *clivosus*. General colour bright clear buffy, about as in *rufus* and in *gracilis angelus*, much paler and clearer than in *butleri* and *clivosus*. Upper surface near "warm buff," darkened a little along the median basal area, clearer on the sides. A patch behind eye and another behind ear white. Ears buffy. Hands and feet white; soles brown with well-marked hair-band. Tail pale buffy above, white below, its terminal third with a brown pencil.

Skull distinctly smaller than that of *T. clivosus*.

Dimensions of the type (measured in the flesh):—

Head and body 106 mm.; tail 149; hind foot 30; ear 18.

Skull: greatest length 34; condylo-incisive length 30; nasals 13.3; palatine foramina, anterior 5.4, posterior 3.7; bulla 10; upper molar series 5.

Hab. Plains of Darfur, round and to the east of El Fasher. Type from Um Kedada, about 100 miles E. of the capital.

Type. Adult female. B.M. No. 23.1.1.143. Original number 1160. Collected March 15, 1922.

The bright buffy colour of this Gerbil distinguishes it from *butleri* and *clivosus*, while from the equally bright *rufus* it differs by its smaller size and the presence of hair-bands on its soles.

34. *TATERILLUS RUFUS* Wettst.

Tatera rufa Wettstein, *t. c.* p. 111.

♂. 479, 493, 506, 1080, 1169. ♀. 507. W. of El Fasher.

♀. 1166. Um Kedada, 100 miles E. of El Fasher.

♀. 1090. Jebel Maidoh. 2750'.

Dr. Wettstein has in our opinion laid too much stress on the presence of the hair-band on the sole as diagnostic of the genus *Taterillus*, while quite ignoring the length of the posterior palatal foramina. It is clear from his excellent photographs that his *Tatera rufa* has the long foramina characteristic of *Taterillus*,

while, as Thomas has shown, *Taterillus* is often without the hair-band.

In this species the sole is whitish and generally completely naked, the ears are unusually large, and the general colour is particularly bright and vivid.

T. gyas Thos., from the Dinder River, is related to *T. rufus*, but is larger.

"Soles of feet white."—W. P. L.

35. *TATERILLUS BUTLERI* Wrought.

♂. 1200, 1202, 1206. ♀. 404, 404*, 1199, 1201. El Obeid and neighbourhood.

♀. 409, 1189. Near Nahud, Kordofan.

A rather dark form with comparatively short tail.

36. *GERBILLUS PYGARGUS* F. Cuv.

♂. 1091. ♀. 1092, 1104. Jebel Maidob. 2750'.

♀. 1083. El Fasher.

37. *GERBILLUS AGAG* Thos.

♀. 406, 408. Nahud, Kordofan.

♀. 413, 414, 415. 100 miles W. of Nahud.

♀. 423. 65 miles E. of Nahud.

♂. 445, 476, 1060, 1129, 1148. ♀. 451, 474, 475, 476, 486, 487, 503, 1079, 1081, 1085, 1126, 1130, 1132, 1133, 1136, 1137, 1146, 1156, 1157. El Fasher and neighbourhood.

♀. 1168. Um Kedada, Darfur.

Hitherto only known from the type, a male obtained in November 1902, at Agageh Wells, by Capt. Dunn.

38. *GERBILLUS NANCILLUS*, sp. n.

♀. 425. 16 miles E. of El Fasher.

♀. 1078. 45 miles N. of El Fasher.

A minute species smaller than any hitherto known.

Size even less than in *Dipodillus henleyi*. General colour above very pale gerbil-colour; only a narrow dorsal area with the usual dark bases to the hairs, those of the flanks with white bases and buffy tips. Under surface snowy-white, the white area taking in the whole of the fore limbs. Middle of face buffy; cheeks, a ring round the eyes, patch at base of ears, and another behind them white. Ears small, their proectote contrasted brown, with the tip whitish, their metectote buffy. Soles of hind feet partly naked behind, but with the hairy terminal part of metatarsus characteristic of *Gerbillus*. Tail practically white, the upper surface very slightly more buffy, the end lightly pencilled with brown.

Skull with proportionally large brain-case and short muzzle. Bulla fairly large, much smaller than in *Dipodillus henleyi*.

Dimensions of the type (measured in the flesh):—

Head and body 54 mm.; tail 79; hind foot 17·5; ear 11.

Skull: greatest length 20·5; condylo-incisive length 17; nasals 7·1; breadth of brain-case 10·2; anterior palatine foramina 3·2; posterior palatine foramina 2·2; bulla 7; upper molar series 3·2.

Hab. Plains of Darfur. Type from 45 miles N. of El Fasher.

Type. Adult female. B.M. No. 23.1.1.169. Original number 1078. Collected February 6, 1922.

This pretty little Gerbil reminds one of the tiny *Dipodillus henleyi* of Lower Egypt, but the soles, though partly naked behind, are distinctly those of *Gerbillus*, in which genus this is much the smallest species known.

39. DIPODILLUS LOWEI, sp. n.

♂. 566, 577, 583, 587, 595, 600, 601, 603, 605, 625, 676, 677, 678, 679, 684, 685, 975, 979, 981, 986, 990, 992, 995, 1005, 1010, 1105.

♀. 564, 565, 578, 581, 582, 584, 588, 591, 592, 593, 594, 602, 604, 618, 620, 624, 674, 675, 680, 681, 688, 689, 693, 694, 906, 973, 976, 978, 980, 982, 983, 984, 987, 988, 989, 991, 993, 995, 997, 998, 999, 1000, 1002, 1004, 1007, 1008. Jebel Marra. 6650'–9750'.

A dark-coloured mountain form of the *D. campestris* group.

Size about as in *D. campestris*. General colour dark, much darker than the clear gerbil-colour of most members of this genus, though occasional or younger specimens of *campestris* are similar. Back dark buffy grizzled with the brown tips of the hairs, the general tone near "Brussels-brown," while some specimens even approach sepia. Sides a little clearer buffy. Under surface as usual wholly white. Ears brown, with the conspicuous whitish markings behind eyes and at base of ears. Legs buffy brownish; hands and feet white. Tail with a fairly well-developed blackish tuft on its terminal third, its hairs ordinarily attaining 8–9 mm. in length; under surface of tail dull buffy brownish.

Skull, on the whole, like that of *D. campestris*, but rather more robust, and the zygomatic plate projecting slightly further forward, so that its anterior point stands about 3·5 instead of 3·0 mm. in front of the base of the notch, as viewed from above. The bullæ are of about the same length, but, apparently owing to a less convex inner side, the slit between them and the front part of the basioccipital is nearly invariably broader. Molars slightly heavier.

Dimensions of the type (measured in the flesh):—

Head and body 110 mm.; tail 143; hind foot 25·5; ear 17.

Skull: greatest length 31·5 mm.; condylo-incisive length 28·5; zygomatic breadth 15·7; nasals 12·5; palatal foramina 6·3; bulla 9; upper molar series 4·4.

Hab. Jebel Marra, above 6000'. Type from 9500'.

Type. Adult female. B.M. No. 23. 1. 1. 212. Original number 982. Collected December 3, 1921.

"Lives under rocks; feeding on grass and flower-seeds. These animals appear to be strictly nocturnal."—W. P. L.

This Gerbil is of considerable interest, for while it is nearly allied to the Algerian and Saharan *D. campestris*, no relative of it is recorded from anywhere near Darfur; nor did the Lynes-Lowe expedition obtain a single specimen of the group in all the low country round Jebel Marra, so that we may be confident that it is really isolated high up on the mountain. In the plains its place would seem to be taken by *Taterillus butleri*, which, like other Gerbils, is pale sandy-coloured, while the present animal has become darkened to suit its rocky environment. Just as has happened with *Lemniscomys lynesi* and other members of the mountain fauna.

We have much pleasure in naming it after Mr. Willoughby Lowe, to whose energy the great extent of the Darfur mammal collection is mainly due.

40. *DIPODILLUS PRINCIPULUS*, sp. n.

♀. 1119. El Malha, Jebel Maidob, N. Darfur. 2700'.

♂. 1127. 90 miles N.E. of El Fasher.

A bright buffy species with long tail and swollen brain-case.

Size medium, about as in *D. stigmonyx*. General colour bright sandy buffy, without the slight dorsal darkening generally found in *stigmonyx*. Sides and posterior part of rump above tail without slaty bases to the hairs, these being white with buffy tips. A white patch behind eye and another behind ear. Ears buffy. Hands and feet white, the soles naked. Tail longer and rather more bushy than in *stigmonyx*, the upper surface lined buffy brown, the lower side white; terminal two-fifths with a well-marked brownish pencil.

Skull about as long as in *stigmonyx*, but much more swollen posteriorly, the brain-case more convex above and considerably broader; bullæ much larger. Palatal foramina shorter. Molars about as in that species.

Dimensions of the type (measured in the flesh):—

Head and body 73 mm.; tail 115; hind foot 21; ear 11.

Skull: greatest length 26·3; condylo-incisive length 23; zygomatic breadth 14·5; breadth of brain-case 13; height from crown to lowest point of bulla 10·8; palatal foramina, anterior 4·1, posterior 2·4; bulla 10×5·5; bi-meatal breadth 14; upper molar series 3·5.

Hab. N. Darfur. Type from El Malha, Jebel Maidob. 2700'.

Type. Adult female. B.M. No. 23.1.1.218. Original number 1119. Collected 10 February, 1922.

The members of the genus *Dipodillus* may be arranged according to the extent to which the brain-case and bullæ are swollen up in proportion to the face, or are of more or less normal Murine development. This species and the much smaller *D. henleyi* are at the swollen-headed end of the series; then among Egyptian species follows *amœnus*; then *stigmonyx* with its allies or synonyms *luteolus* and *bottæ*, and the smaller-toothed *watersi*. Then comes *campestris* and its ally *lowei*; and finally, and most extremely murine, the small species next to be described.

This pretty and distinct species is one of the few novelties resulting from the visit of the Expedition to the black rocky mountain Jebel Maidob, in N. Darfur, whose mammal fauna has proved far less striking than that of Jebel Marra.

41. *DIPODILLUS MURICULUS*, sp. n.

♂. 1082. Madu, 80 miles N.E. of El Fasher. 2900'.

A small species with a very murine-shaped skull.

Size very small, considerably less than in *principulus*, little larger than in *henleyi*. General external characters as in *principulus*, except for the markedly shorter tail. Colours as described in *principulus*, with similar white bases to the lateral and anal hairs. The general tone is, however, more strongly buffy, but how far this is affected by the only specimen being tinted with the reddish sand of its locality, we are unable to say. Eye and ear markings present. Hinder soles quite naked. Tail much shorter than in *principulus*, scarcely pencilled, the proximal portion thinly haired and showing the scales.

Skull, for a Gerbilline, of a remarkably murine shape, the cranial region neither broadened nor inflated and the bullæ small, so that at first sight, at least from above, the skull might be taken for that of a *Mus*. Supraorbital edges well marked. Palatal foramina narrow. Bullæ comparatively small, oval, the mastoid portion almost without inflation.

Teeth apparently as usual, but much worn in the only specimen.

Dimensions of the type (measured in the flesh):—

Head and body 65 mm.; tail 82; hind foot 18; ear 12.

Skull: greatest length 23 mm.; condylo-incisive length 20; zygomatic breadth 12; nasals 8.5; interorbital breadth 4; greatest breadth of brain-case 10.3; height from crown to lowest point of bulla 8.8; palatal foramina, anterior 3.7, posterior 2.1; bulla 7.5 × 4.5; bi-meatal breadth 10.6; upper molar series 3.1.

Hab. as above.

Type. Old male. B.M. No. 23.1.1.220. Original number 1082. Collected 3 February, 1922.

A very striking little Gerbil, distinguishable by its short tail and very murine skull.

42. *DESMODILLISCAUS BRAUERI* Wettst.

♂. 1192. 75 miles W. of El Obeid.

♀. 1172. 140 miles E. of El Obeid.

The type of this remarkable little Gerbil was described from El Obeid. These almost topotypical specimens are most welcome additions to the collection.

They show that the Nigerian species *D. buchanani* is more nearly allied to *braueri* than we had supposed, as the difference that we had observed in the first lower molar seems to be only due to Dr. Wettstein's photograph having been taken at an angle which gave a misleading outline to the tooth. And as to the difference in the bullæ, those of *buchanani* had had the meatal inflation broken off, an accident which was only perceived on the examination of the present specimens. But the two species are, however, still distinguishable by the greater size of the molars of *buchanani*—3.2 mm. in length above as compared with 2.9*.

43. *STEATOMYS AQUILO*, sp. n.

♀. 1013. Niurmeya, Jebel Marra. 7000'. Collected 23 December, 1921. B.M. No. 23. 1. 1. 438. *Type*.

A small species related to the Nigerian *cuppedius*.

Size about as in *cuppedius*. General colour above pale wood-brown, washed laterally with buffy. Under surface white, less sharply defined than usual. Face rather more buffy than back. Ears brown with a small whitish patch behind them. Forearms and hands, and hind feet white. Tail brown above, whitish below.

Skull very much as in *cuppedius*, but the palatal foramina longer, extending nearly to the level of the middle lamina of *m*¹ and narrower.

Incisors unusually strongly bevelled, so much so that in side-view the part of the tooth behind the groove appears little broader than that in front. In the type the upper incisors are white, but we suppose this to be due to some accidental chemical deterioration; the lower ones are yellow as usual.

Dimensions of the type (measured in the flesh):—

Head and body 69 mm.; tail 39; hind foot 14; ear 13.

Skull: greatest length (c.) 19.5; nasals 7.5; interorbital breadth 4; front of incisors to back of *m*³ 9.7; palatal foramina 4.5; upper molar series 3.7.

Hab. and *Type* as above.

"Found dead on native trail with throat cut."—W. P. L.

This represents the most northern occurrence of the genus *Steatomys*, although on the west side of Africa it ranges nearly as far—to Kano, Nigeria. The species would seem to be nearly allied to *S. cuppedius*, unless the peculiar white coloration of the

* Alveolar lengths—*buchanani* 3.7, *braueri* 3.2–3.4 (Wettstein 3.5).

upper incisors is a normal character, a point which can only be settled on the arrival of further specimens.

[The description of the following *Steatomys*, distinguished and labelled some years ago, seems accidentally never to have been published :—

Steatomys gazella, sp. n.

A large species, with large bullæ and very large molars.

General colour above dark wood-brown, darker than in most species. Under surface white, but only along a narrower area than usual. Ears dark brown, without postaural whitish patch. Hands and feet dull whitish.

Skull of about the same large size as in *pratensis* and *caurinus*, but the bullæ larger than in either, and the molars very much larger. Palatal foramina long, widely open.

Dimensions of the type (measured on the skin):—

Head and body (c.) 100 mm.; tail 52; hind foot 18.5.

Skull: greatest length 26 mm.; condylo-incisive length 24.5; palatilar length 12.2; palatal foramina 5.4×2.4 ; bulla 6.3; upper molar series 4.7.

Hab. Bahr-el-Ghazal; type from Tamburas.

Type. Adult male. B.M. No. 5.10.7.4. Collected and presented by Maj. H. Bray.

Readily distinguishable by its large size and very large molars.]

44. *RATTUS* (*MASTOMYS*) *MACROLEPIS* Sund.

♂. 453, 471, 505. ♀. 452, 472, 496, 497, 500. El Fasher.

♂. 510, 518, 519. ♀. 511, 512, 514, 515, 532, 533, 534, 535, 536, 538, 540, 1021, 1022, 1026, 1033, 1034, 1035. N.E. Jebel Marra. 5500'.

♂. 542. ♀. 543, 1023, 1027. N.W. Jebel Marra. 6000'.

♂. 637, 668, 703, 704. ♀. 634, 635, 636, 640, 646, 650, 651, 652, 654, 659, 662, 667, 669, 701, 702. Foot-hills, S. Jebel Marra. 4000'.

♂. 970. ♀. 962, 972. S.E. Jebel Marra. 8000'.

♂. 621, 623. ♀. 622. S.W. Jebel Marra. 6650'.

♂. 554, 561. ♀. 551, 555, 556, 558. Niurmya, Central Jebel Marra. 7100'.

♂. 619, 710, 713, 719. ♀. 546, 547, 579, 580, 613, 714, 715, 716, 717, 964. Central Jebel Marra. 5000'–7900'.

♂. 724, 940, 947, 956. ♀. 723, 756, 938, 952, 961. Zalingei. 3300'.

♂. 634, 763, 769, 776, 778, 782, 785, 786, 787, 789, 792, 797, 798, 805, 806, 810, 812, 813, 816, 822, 825, 831, 835, 838, 839, 840, 842, 851, 863, 867, 868, 871, 912.

♀. 730, 731, 732, 761, 764, 772, 775, 780, 790, 793, 815, 821, 828, 841, 845, 858, 870, 901, 921. Kulme, Wadi Aribo. 3300'.

♀. 1182. Nahud, Kordofan.

♂. 1203. ♀. 1204. Abu Heraz, Kordofan.

A very fine series of these difficult field-mice, which will be of great use when a closer study can be made of the group. There is considerable variation in size among them, and perhaps more than one form is included.

The two members of the subgenus *Mastomys* in this region are respectively this wild-living form, more or less rufous, with a white or whitish sharply defined underside, and a house-haunting race, dark smoky grey, with little-defined dull greyish-buffy belly—indeed, corresponding closely in colour to house-haunting *Mus musculus*. A co-type of Sundevall's *Mus macrolepis* in the British Museum (No. 46. 6. 2. 58) certainly agrees more with the former than the latter, and we have therefore used that name for the species. We also consider that Wagner's *Mus limbatus* should be placed as a synonym of it.

45. *RATTUS* (*MASTOMYS*)—*ugandæ* group.

♂. 779, 866, 898, 899, 900, 904, 908, 913, 916, 917, 924.
♀. 780, 843, 853, 895, 897, 902, 905, 910, 925, 927. Kulme, Wadi Aribi. 3300'.

♂. 513, 643, 1017, 1030, 1031. ♀. 1016, 1018, 1024, 1028. Jebel Marra at various altitudes.

♂. 879. ♀. 938, 953. Zalingei. 2800'.

The house-haunting members of *Mastomys* are very much alike all over Northern Africa, and may even be all of one species. For the present, however, we do not venture to give an exact determination of these specimens.

46. *ACOMYS* *WITHERBYI* de Wint.

♂. 420, 428, 448, 477, 1059, 1138, 1142, 1177. ♀. 421, 429, 430, 431, 432, 433, 437, 438, 449, 455, 1070, 1076, 1093, 1125, 1139, 1140, 1143, 1145. El Fasher and neighbourhood.

♀. 1036. Kurra, Jebel Marra. 5200'.

♂. 606. Niurmeya, Central Jebel Marra. 7100'.

♀. 1121. Near Togato Hills.

♂. 407, 1184. ♀. 1119, 1183. Neighbourhood of Nahud.

♂. 403, 405, 1190, 1195, 1196. ♀. 1191. El Obeid and neighbourhood.

♂. 1020. N.E. Jebel Marra. 6500'.

♂. 1096, 1099, 1100, 1107, 1108, 1115, 1116, 1117, 1118.

♀. 1097, 1101, 1103, 1109, 1111, 1113. Jebel Maidob. 2700'.

47. *ARVICANTHIS* *TESTICULARIS* Sund.

♂. 1021, 1042, 1044, 1045, 1046, 1050, 1051, 1052, 1053, 1054, 1055, 1057, 1066. ♀. 434, 439, 440, 442, 454, 1039, 1040, 1041, 1043, 1047, 1048, 1049, 1056, 1074. El Fasher.

♂. 1067, 1072, 1075. ♀. 1073. 35 miles N. of El Fasher.

♂. 630, 664. ♀. 629, 697, 709. South Jebel Marra.

♀. 562. Niurmya, Central Jebel Marra.

♀. 517, 1025. N. Jebel Marra.

♂. 720, 741, 742, 935, 942, 962. ♀. 725, 727, 936, 947.
Zalingei.

♂. 768, 833, 896. ♀. 767, 884. Kulme, Wadi Aribò.

♂. 1110, 1120. Jebel Maidob.

♀. 1205. El Obeid, Kordofan.

48. *LEMNISCOMYS DUNNI* Thos.

♂. 1158, 1170. ♀. 435, 441. El Fasher.

♂. 1009, 1029. ♀. 541. Jebel Marra. 5200'–7700'.

♀. 1162, 1163, 1164, 1167. Um Kedada.

Fully agreeing with the type, which was obtained by Col. Dunn in the Kaga Hills in 1902. The species is apparently common on the plains of Darfur including the lower slopes of Jebel Marra, while it is replaced higher up on that mountain by *L. lynesi*.

Nearly related to it is the following form from the Nuba region of Southern Kordofan :—

LEMNISCOMYS DUNNI NUBALIS, sp. n.

Similar in essential characters, in size and spininess of form, to true *dunni*, but the colour throughout much intensified, the stripes and other parts, which in *dunni* are pale buffy, very strong and rich buffy, almost ochraceous. Ears very deep buffy. Under surface buffy laterally instead of white.

Skull as in *dunni*.

Dimensions of type :—

Head and body 103 mm.; tail 130; hind foot 24; ear 14.

Skull: greatest length 29·5; condylo-incisive length 26·7; bulla 6; upper molar series 5.

Hab. Nuba Country, Southern Kordofan. Type from Talodi. 1300'.

Type. Adult female. B.M. No. 18.7.2.14. Original number 5. Collected 21 February, 1917, and presented by Maj. C. Graham. Three specimens.

Lemniscomys zebra Heugl., of which Thomas has examined the type, has a wholly white underside, and is clearly a member of the other group of this genus, with much darker-coloured fur and smaller bullae. To this latter group the next species belongs.

49. *LEMNISCOMYS LYNESI*, sp. n.

♂. 617, 690, 967. ♀. 563, 590, 598, 691, 968, 1003, 1006, 1011. Jebel Marra, at altitudes from 7700' to 9750', and to the crater.

A dark species with comparatively long soft fur.

Size fairly large. Fur comparatively long, and much softer and more spineless than in any allied species. General colour

dark, the light lines dull whitish, with a distinct tendency to break into spots. Under surface buffy whitish, the bases of the hairs broadly slaty, except on the chin. Ears dull ochraceous, a richer ochraceous tuft at their anterior base. Hands and feet dull buffy whitish. Tail black above, dull buffy whitish below.

Skull with distinctly smaller bullæ than in *L. dunni*.

Dimensions of the type (measured in the flesh):—

Head and body 112 mm.; tail 125; hind foot 25; ear 17.

Skull: greatest length 29; condylo-incisive length 26.6; palatal foramina 5.1; bulla 5; upper molar series 5.3.

Hab. Jebel Marra, at various altitudes, from 7000' upwards to the crater. Type from Central Jebel Marra on western slope, 8000'.

Type. Adult male. B.M. No. 23.1.1.313. Original number 617. Collected March 22, 1921.

This distinct mountain species is readily distinguished by its comparatively long soft fur, which is practically without spines, in marked contrast with both *L. dunni* and *zebra*. Also by the slaty bases to its belly-hairs and by its small bullæ.

On freshly-killed specimens the attention of both collectors was specially attracted to this animal by the greenish iridescent sheen on its fur, though, as with so many mammals, this sheen fades away in the dried skin.

We have much pleasure in naming this well-marked species in honour of Admiral Lynes, to whose enthusiasm and scientific spirit the National Museum owes the present magnificent accession to its collections.

50. GRAMMOMYS ARIDULUS, sp. n.

♂. 826. Kulme, Wadi Aribo. 3300'.

An unusually pallid, desert-coloured species.

General colour of dorsal surface dull ochraceous lined with dark brown, brightest and clearest upon the flanks and rump. At the rump the tint is near Ridgway's "ochraceous-tawny." Top of head and nape duller and greyish. Region between eye and ear on each side grey. A small white patch behind each ear. Ears bright ochraceous tawny within and without, save for a marginal band of dark reddish brown extending from the base of the preectote to the tip of the ear. Underparts cream, in sharp contrast with flanks. Outer surface of forearms and upper surfaces of hands and feet cream-buff. Tail bicolored, dusky above, whitish below.

Skull most nearly resembling that of *G. buntingi*, described from Liberia, in form, but distinguished chiefly by its larger bullæ and heavier molars.

Dimensions (measured in the flesh):—

Head and body 115 mm.; tail 175; hind foot 24; ear 18.

Skull: condylo-incisive length 26.6; extreme length 29.4;

zygomatic breadth 14.4; interorbital construction 4.3; cranial width 12.8; dental length 13.5; cheek-teeth (crowns) 4.2.

Type. Old male. B.M. No. 23.1.1.324. Original number 826. Collected July 22, 1922, at Kulme, Wadi Aribo, Darfur. Altitude 3300'.

Hab. as above.

This is a very well-marked species distinguished by its bright coloration from all forms previously described. In outward appearance it is perhaps more like *G. s. elgonis* than any other, while in skull it resembles the outwardly very different *G. buntingi*.

51. LEGGADA TENELLA Thos.

♂. 400. 30 miles W. of El Obeid.

♂. 627. ♀. 628. Foot-hills, S.W. Jebel Marra. 4500'.

♂. 712, 718. South Central Jebel Marra. 4000'.

♂. 599. Central Jebel Marra. 9750'.

♀. 587. Niurmya, Central Jebel Marra. 7150'.

♂. 695, 818, 824. ♀. 903. Kulme, Wadi Aribo. 3300'.

52. JACULUS GORDONI Thos.

♀. 14. Near El Fasher. 2600'. May 1920 (20.7.30.17).

Incisor-bulla length 35.0 mm.

53. JACULUS JACULUS Linn.

♂. 1135. 55 miles N.E. of El Fasher.

While it is not unnatural that the Kordofan *J. gordonii* should be found in Darfur, the capture of this specimen, clearly referable to *J. jaculus*, so close to where the same collector found the first-named species in 1920, is worthy of note. Moreover, within the species *J. jaculus*, it has not the warm colour of the Khartoum *J. j. butleri*, but is very similar to the more buffy *J. j. jaculus*, which therefore would seem to range along the deserts to the west of the Nile as far south as Darfur. The nearest previous record for this form is Dongola.

54. LEPUS HAWKERI Thos.

♀. 1198. 50 miles W. of El Obeid.

♂. 410. 70 miles W. of Nahud.

♀. 422. 75 miles E. of El Fasher.

♂. 721, 736, 747, 757, 951. ♀. 737, 748. Zalingei, Darfur. 2800'-3000'.

♂. 692. ♀. 632. Foot-hills, S. of Jebel Marra. 4000'.

♀. 1014 juv. Niarmya, Jebel Marra. 7000'.

♂. 696. Deriba Lakes, Jebel Marra. 7400'.

♀. 977. Jebel Marra. 9500'.

♀. 765 juv., 808. ?sex. 796 juv. Kulme, Wadi Aribo. 3300'.

These agree very well with the type of *L. hawkeri*, described from Kaka, Sudan. *L. hawkeri* would seem to be the representative of *isabellinus* ("*æthiopicus*") in the open country west of the Nile.

55. *PHACOCERUS ÆTHIOPICUS* subsp.

♂. 800. Kulme, Wadi Aribo. 3300'.

♀. 728 juv., skull only. Kulme, Wadi Aribo, 3300'.

Not improbably referable to *P. æthiopicus fossor* Schwarz., described from the Bagirmi District.

56. *ALCELAPHUS LELWEL TSCHADENSIS* Schwarz.

♂. 760. Kulme, Wadi Aribo. 3300'.

♂. 777, skull and head-skin only. Kulme, Wadi Aribo. 3300'.

♂. 856. Kulme, Wadi Aribo. "Skull, tail, and fore and hind legs only—the latter to show the black markings, which are unusually pronounced for these parts. Chin always black."

57. *SYLVICAPRA GRIMMIA PALLIDIOR* Schwarz.

♂. 644, 638. Foot-hills, S. Jebel Marra. 4000'. "Tolerably common on dry stony hill-sides."

♀. 823, 849. Kulme, Wadi Aribo. 3300'.

♀. 752. Zalingei, Darfur, Sudan. 2800'. "Native name 'Digi-dig.'"

A very distinct form, of which we have had no satisfactory material previously. Characterized by its pale colour and large size.

58. *OUERBIA OUREBI SPLENDIDA* Schwarz.

♂. 852. ♀. 791. Kulme, Wadi Aribo. 3300'.

"Found very sparingly in wooded country. Native name, 'Gazella amma.'"

The female captured on July 2 contained a well-developed foetus.

As the collectors noted, the female differs from the male in having a dark patch on the head.

59. *GAZELLA RUFIFRONS* Gray.

♀. 589. Central Jebel Marra. 10,000'. "Shot from a lot of 5 on plateau."

♂. 811. Kulme, Wadi Aribo. 3300'.

♂. 1181. Head only. 205 miles E. of El Fasher. "Rarely seen here and further E. along the road."

We are not at present prepared to determine this material subspecifically.

60. *GAZELLA DORCAS* Linn.

- ♂. 1058. 10 miles N. of El Fasher. Horns $11\frac{3}{4}$ ".
 ♂. 1094, 1095. 150 miles N.E. of El Fasher.
 ♂. 1147, skull only. 19 miles N. of El Fasher.
 ♂. 469. ♀. 470. Skulls only. 35 miles E. of El Fasher.
 ♀. 427. 10 miles E. of El Fasher.
 ♀. 1149, 1150. Near El Fasher.
 ♀. 915, no skin. Wadi Aribo.

61. *PROCAVIA RUFICEPS* H. & E.

- ♂. 1065. ♀. 1063, 1064. 35 miles N. of El Fasher.
 ♀. 1131. 60 miles N.E. of El Fasher.
 ♀. 773, 819. Kulme, Wadi Aribo.
 ♂. 957, 958. ♀. 880, 959, 960. Zalingei.
 ♂. 1098. Jebel Maidoh.

Native name, "Bogos."

62. *PROCAVIA RUFICEPS* MARRENSIS, subsp. n.

- ♂. 665. ♀. 670. Foot-hills of Jebel Marra. 4000'.
 ♂. 552, 559, 516, 1012. ♀. 553, 566, 608. Jebel Marra.
 7100'.
 ♂. 527. ♀. 526, 528. Jebel Owi, N.E. Jebel Marra.
 6500'.

Rather larger on the average than true *ruficeps*; the fur longer, the colour darker, and the dorsal patch less conspicuous, more overlaid with the dark ends to the dorsal hairs. General colour approximating to "Saccardo's umber," but often darker, and always darker than the average in true *ruficeps*. Nape dark brown, like the crown. Hairs of back broadly tipped with blackish brown in a specimen in good pelage. Hind back and rump and the thighs dark brown. Under surface dull buffy, darker than in *ruficeps*.

Skull averaging larger than in *ruficeps*.

Dimensions of type (measured in the flesh):---

Head and body 504 mm.; hind foot 71; ear 30.

Skull: condylo-basal length 91.5; zygomatic breadth 55; front of p^1 to back of m^3 (teeth much worn) 33.

Hab. Jebel Marra. Type from the central part of the mountain at 7100'.

Type. Old male. B.M. No. 23.1.1.486. Original number 616. Collected March 19, 1921.

This is a dark mountain race of the widely spread *P. ruficeps* of the Soudan. It is unusually variable in colour, but certainly averages considerably darker than the Dassie of the plains.

19. On a Remnant of the Omphalo-mesenteric Arteries in the Manatee. By K. KOSTANECKI, M.D., LL.D., F.Ac.Sc. Cracow*.

[Received February 19, 1923: Read April 10, 1923.]

(Text-figure 1.)

In a paper published in 1897 in the Proceedings of the Zoological Society (Notes upon the Anatomy of a Manatee, *Manatus inunguis*), Beddard describes and represents in a drawing the cæcum of this animal. The general shape of the cæcum is precisely like that of the other species of Manatee, especially of *Manatus latirostris*, one specimen of which Beddard has also examined, and which previously had been described by Murie†. Beddard adds: "I should not have had the drawing prepared were it not for a peculiar fold of mesentery which it is the main purpose of that sketch to illustrate. This fold, which is not referred to by Dr. Murie, lies on either side of the mesentery supporting the ileum and runs nearly to the cæcum. It does not bear a blood-vessel, and the fold of either side is continuous with its fellow by a complete bridge over the front side of the ileum as indicated in the sketch. Both species are precisely alike in the presence and in the relations of these two mesenteries." (The drawing in Beddard's paper is also reproduced in Weber's 'Säugetiere'.)

Neither Beddard nor Weber gives an explanation of this fold.

I have had the opportunity of examining a Manatee fœtus (*Manatus inunguis*) 35 cm. in length in the collections of the Royal Museum of Natural History at Brussels, thanks to the kindness of Prof. Dollo.

The cæcum presented the aspect known in the adult animals from the papers of Cuvier, Owen, Home, Murie, Flower, Rapp, Huntington, Beddard, Waldeyer, and others.

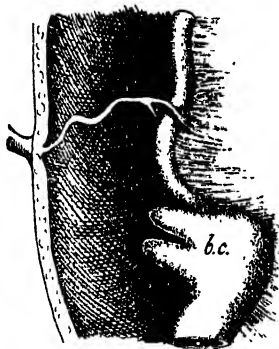
I noticed immediately a few cms. away from the cæcum the bilateral folds described by Beddard, which ran from the dorsal mesentery to the wall of the ileum, uniting on its ventral, antimesenteric wall. However, they did not terminate there in a narrow bridge, as in Beddard's drawing, but the central part was markedly elevated above the surface of the ileum, and was elongated into a narrow strip stretching towards the umbilicus and terminating there (as can be seen in the text-figure, p. 274).

* Communicated by THE SECRETARY.

† Murie, "On the Form and Structure of the Manatee," Trans. Zool. Soc. viii. p. 127.

The connection of these folds with the umbilicus furnishes an immediate explanation of the condition in the adult animal described by Beddard. Without any doubt, we have before us a remnant of the involution of the vitelline duct and its blood-vessels, especially its arteries. I have not been able to dissect the precious specimen and make microscopical sections, but examining the strip and its relation to the ileum, I noticed that the wall of the ileum between these folds was smooth; the vitelline duct had completely disappeared, and blood-vessels were not apparent under the peritoneum forming these folds; it may be that microscopical sections would have disclosed degenerated remains of the walls of these vessels. In spite of that, there can be no doubt, considering the course of this strip, that it owes its existence to structures connected with the yolk-sac apparatus.

Text-figure 1.



Caecum and umbilicus of Manatee.

b.c.=bifid caecum.

Especially regarding the symmetrical origin of the two folds from the dorsal mesentery of the terminal portion of the ileum, there can be no doubt that these are produced by the omphalo-mesenteric arteries. The omphalo-mesenteric or vitelline vein or its remains cannot play any part here; in fetal life it runs differently, namely, from the umbilicus to the mesoduodenum. In the fetus which I have examined it had vanished completely.

The changes of the omphalo-mesenteric arteries are described by several authors, especially in the very exact paper by Broman*, who, together with the results of previous researches, gives many new data.

It is known that the omphalo-mesenteric arteries are originally paired and run on either side of the ileum to the umbilicus, then unite, both in the part which runs through the mesentery,

* Broman, "Über das Schicksal der Vasa vitellina bei den Säugetieren," *Ergebnisse der Anatomie und Entwicklungsgeschichte*, Bd. xxi. (1913).

forming one arteria omphalo-mesenterica, the future superior mesenteric artery, and in the part where, ventrally to the ileum, they run towards the umbilicus; Broman calls this last part—which runs outside of the gut together with the vitelline duct, towards the umbilicus and in the umbilical cord—the vitelline artery.

In some animals the arteriæ omphalo-mesentericæ, though not paired in their proximal and distal parts, remain for some time paired in the part which runs on both sides of the ileum, thus forming a ring around the ileum, which, starting dorsally from the single arteria omphalo-mesenterica, passes on the ventral side of the ileum into the single arteria vitellina, which runs toward the umbilicus in the mesodermic vitelline stalk.

In most animals this part does not remain paired, the artery on one side disappearing (the left in some animals, in others the right), the persisting artery of the other side running on the lateral surface of the ileum, but deviating from its wall, so as to produce a peritoneal fold; usually this fold later on loses its connection with the wall of the ileum and thus, as the beginning of the arteria vitellina, passes on the mesoileum.

When after the disappearance of the vitelline duct, the vitelline artery also disappears, the mesodermal yolk-sac-stalk grows thinner and thinner, ruptures, and finally vanishes.

Broman in the paper I have cited proves that during this process we meet with variable conditions in different animals. Thus, in some animals until birth the vasa omphalo-mesenterica can remain visible always, in others abnormally; but usually they disappear in the fœtus, and leave behind them folds, running towards the umbilicus, which persist in some animals only for a short period of their fetal life, in others until birth and sometimes even in extra-uterine life in the adult animal. These folds, running towards the umbilicus, rupture, and either vanish completely or (either only in fœtus or new-born or adult animals) form bands adherent to the dorsal mesentery, but hanging freely down into the abdominal cavity.

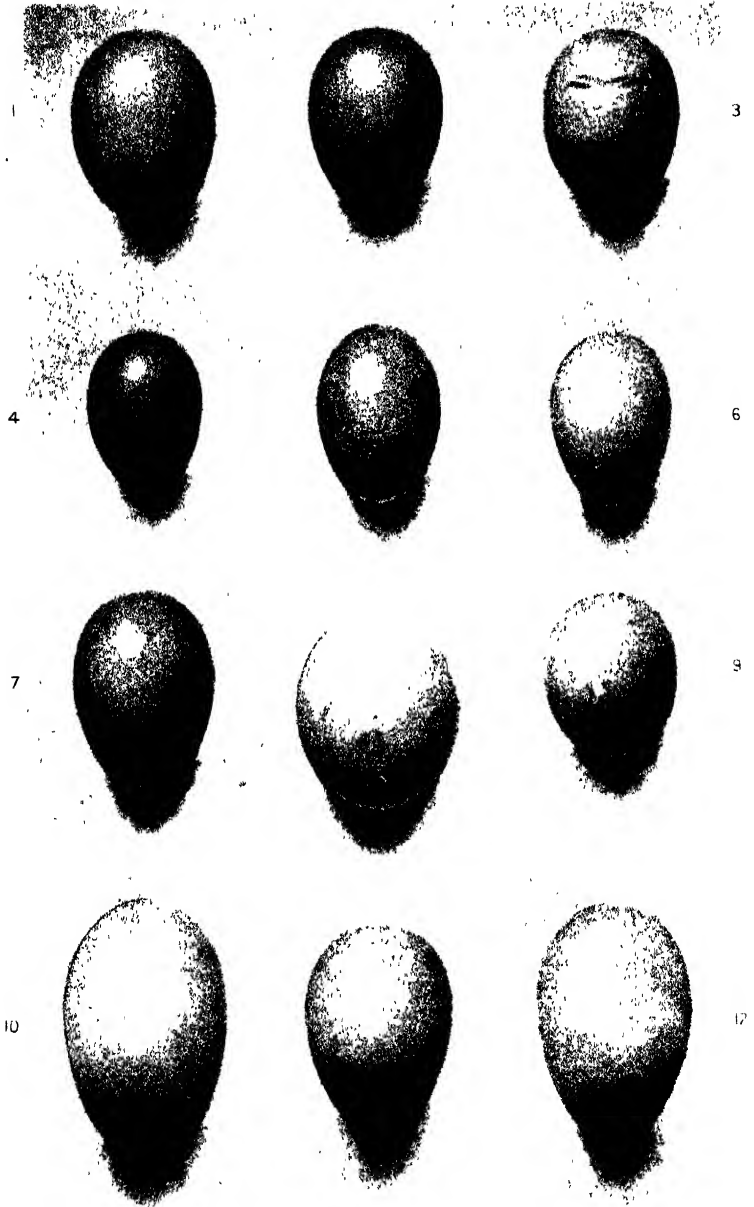
The remains of the vitelline vein which run towards the mesoduodenum, Broman calls "appendix mesoduodeni," the remains of the vitelline artery "appendix mesilei"; any part of the ruptured yolk-duct-stalk remaining near the umbilicus, "appendix umbilicalis."

Broman noticed in an adult *Castor fiber* in the place where in other new-born animals, or their fœtuses, could be seen the appendix mesilei, a remarkable fold, running from one side of the mesileum to the wall of the ileum; he explains it as the remains of the fold, formed by the artery joining the omphalo-mesenteric artery in the mesileum and the arteria vitellina in the yolk-sac-stalk by separating from the wall of the ileum.

I see in this case of *Castor fiber* a complete analogy with the condition in the Manatee, except that in the Manatee, in the place of the appendix mesilei of other animals, such a fold appears on

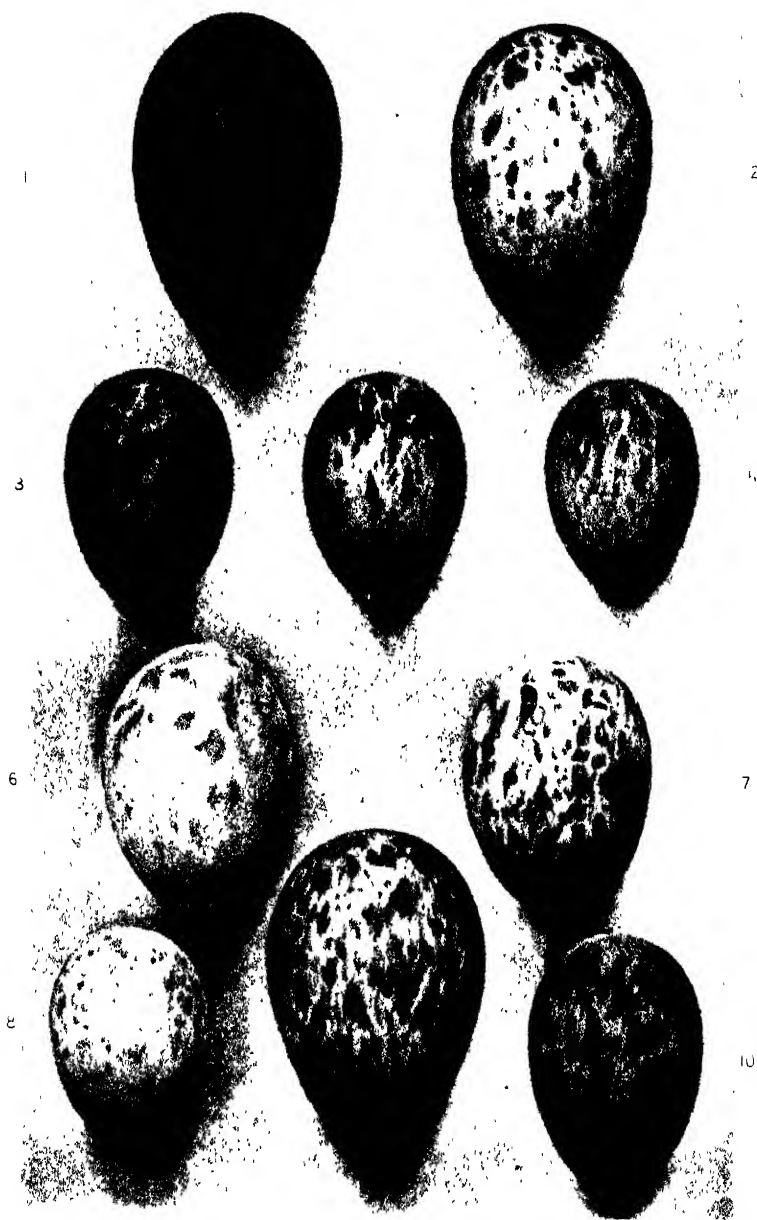
both sides. This shows that in the Manatee the paired parts of the vitelline arteries, which enclose on both sides the ileum, must have persisted for a longer time than in other animals, and, deviating symmetrically from the wall of the ileum, must have formed symmetrical peritoneal folds. As in *Castor fiber* the one-sided fold, so here the paired folds persisted in the adult animal.

The fact, that those paired folds meet on the ventral wall of the ileum, forming a sort of bridge, appears quite natural, considering that the omphalo-mesenteric arteries joined on the ventral wall of the ileum and from there ran toward the umbilicus in the yolk-sac-stalk, which in the foetus which I examined was still preserved.



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CUCKOOS' EGGS AND EVOLUTION

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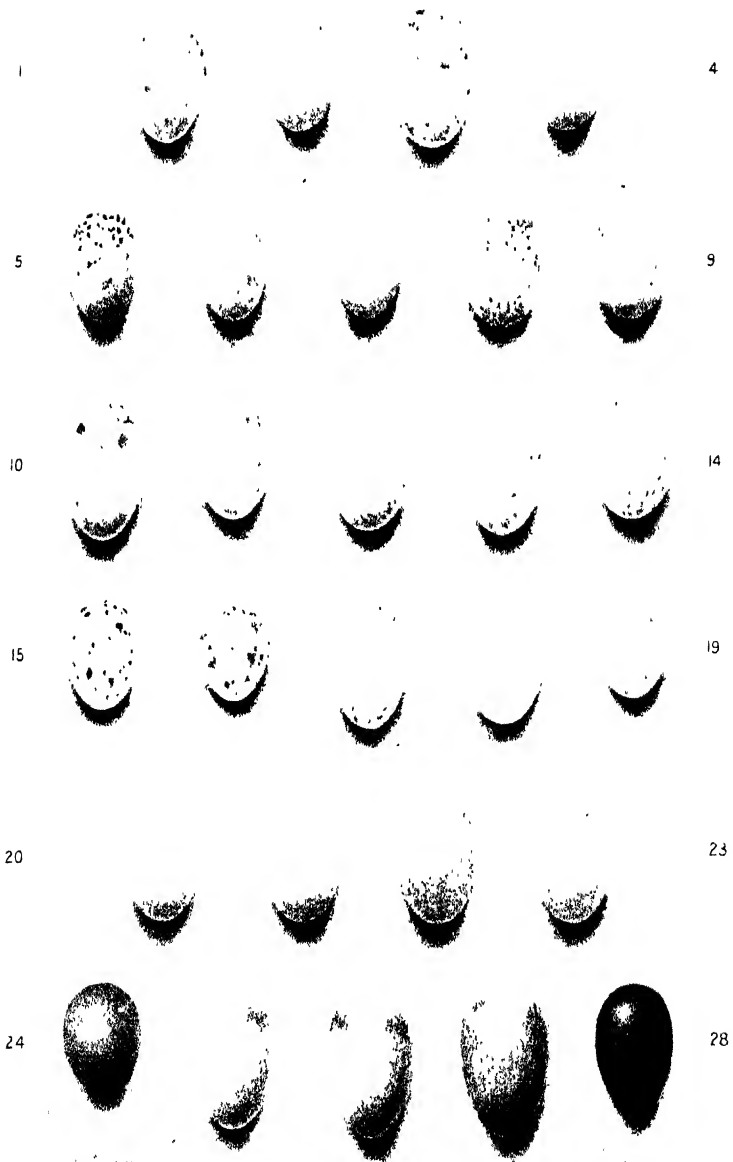
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20. Cuckoos' Eggs and Evolution.

By E. C. STUART BAKER, F.Z.S.

[Received March 19, 1923 : Read April 24, 1923.]

(Plates I.-IV.)*

Much has recently been written on Cuckoos and Cuckoos' eggs, in some cases the writers having laid down laws and accepted facts as proved on very insufficient data. Certain of these writers, who have watched the actions of individual Cuckoos and who have spent much time and money on their valuable observations, have theorized on the presumption that what one Cuckoo does all Cuckoos do. Other writers, also from watching one bird, essay to prove that the former are wrong because their observations do not have the same result as their own. As a matter of fact both are equally correct, the result of their observations are of great value, and their work worthy of all praise so long as they do not pose as authorities, able to prove or disprove theories, until their experiences are far wider.

For over forty years now I have studied Cuckoos, and the older I grow and the more I know about these birds, the more certain I am that I have not yet sufficient data to enable me to do more than roughly outline certain theories and point out what there is in support of them.

Curiously enough, the most interesting of all Cuckoo subjects is the one which seems to have been most avoided. I refer to the evolution of Cuckoos' eggs resembling the eggs of their foster parents sufficiently well to enable them to escape destruction. Perhaps this is because our British Cuckoo, *Cuculus canorus canorus*, is only a very recently evolved type of Cuckoo and within its few thousand years of existence has not yet had time to eliminate those members of its species which lay eggs dissimilar to those of the birds it selects as fosterers. To find really satisfactory instances of perfected or far advanced evolution, or of evolution in an obvious stage of transition, we have to go abroad and examine the eggs of such genera as *Clamator*, *Coccytes*, *Hierococcyx*, etc. Amongst these we may hope to find sufficient evidence to enable us to show what has already taken place and, by analogy, to learn what is probably taking place at the present day amongst other genera and species.

The material from which I have drawn my deductions consists of some 2500 Cuckoos' eggs collected from Europe, Asia, and Australia (not Africa), but principally from India where Cuckoos, of many species, are exceedingly common. As I have already

* For explanation of the Plates see pages 293, 294.

said, this material is insufficient for me to pretend that I have learnt all that there is to know about Cuckoos and their eggs, but it seems sufficient to prove that:—

(1) In some genera and species evolution is only in its earliest stages;

(2) In others it has progressed much further; and

(3) In certain genera and species it has arrived at perfection or finality.

Before proceeding to examine these three conditions in detail, it may be as well to propound the theory of evolution as accepted by me in this connection.

It will be probably generally admitted that the original progenitors of Cuckoos laid white eggs and that they continued to do so for a very long period after all trace of their reptilian ancestry had disappeared. In fact, this persists to the present day amongst those Cuckoos of the genera *Centropus*, *Rhopodytes*, etc., etc., which are not parasitic. The belief of course entails the acceptance of the theory that parasitic Cuckoos have acquired their curious habit and not that non-parasitic Cuckoos have grown out of it. If we accept this theory of an original white or nearly white egg, it will be necessary also to accept the fact that there has been some degree of evolution in almost all parasitic Cuckoos' eggs, for white eggs are very rare amongst Cuckoos and even those which are white are quite different in character to the glossless dead white or yellow-white of most reptiles' eggs. If, however, we accept the theory that all Cuckoos' eggs were originally white, we have again to accept the probability that all other birds' eggs were white and, this being so, we should expect that the Cuckoo's egg would have developed *pari passu* with the eggs of the bird in whose nest it was deposited. Other birds' eggs have acquired certain coloration, shapes, sizes, etc., in each case for some definite purpose which has aided it to escape destruction. In some instances the purpose for which the character has been acquired is obvious. Many birds which lay their eggs on the ground lay such as are beyond doubt protectively coloured; some lay eggs conspicuously coloured to enable the owners to distinguish their own eggs among colonies; others lay eggs so shaped that they cannot roll off narrow ledges of cliffs; yet others lay eggs so large that the chicks emerge fledged and able to take care of themselves from the start, whilst in many other instances we are still too ignorant of the demands of nature to know why the characters exhibited have been acquired.

Why then have not the eggs of all parasitic Cuckoos arrived at the same degree of evolution as those of other birds? Simply because Cuckoos are a modern creation and even amongst Cuckoos the parasitic habit is more modern than the bird and amongst those again which have acquired this habit, some have taken to it later than others.

All sorts of fantastic theories have been advanced as to how

Cuckoos' eggs have attained similarity to those of their fosterers but really this evolution has been brought about in the simplest manner. We may presume that at one time all the eggs of any one particular kind of Cuckoo were white and that they were laid promiscuously in any birds' nests which were handy. If among these there had been a suitable fosterer with white eggs, there would have been little or no evolution or alteration in the Cuckoo's egg. What would have occurred would merely have been that those white eggs placed in fosterers' nests with white eggs would have been hatched in far greater numbers than those which were placed with contrasting eggs and gradually the latter would have been eliminated whilst the former would have survived. This is, indeed, what seems to have happened in a few cases as I will show later on. But in the majority of instances it is evident that there were either no suitable fosterers laying white eggs or that they were not in sufficient numbers to be able to act both as foster-parents to the Cuckoo and also perpetuate their own race. Amongst the Cuckoos' eggs, however, there were probably some which were abnormally coloured with faint blue, red, or some other colour. Now, if these were placed alongside the eggs of foster birds with somewhat similarly coloured eggs, they would escape detection in greater proportion than the quite pure white ones, whilst among the former again those eggs with the deepest tinge would escape more often than the others and so, just by the gradual elimination of the most unfit, we finally obtain a coloured egg so close to that of the fosterer that no further elimination is required.

Evolution in the Cuckoo's egg has, in fact, proceeded as in all other phases of evolution. Destruction and creation are synonymous terms in evolution; the unfit have perished and the more fit survived, the latter in their turn being wiped out as yet better adapted individuals took their place.

In discussing the three degrees of evolution, referred to above, it will probably be more convenient if we examine the third degree, *i. e.*, that of perfect evolution first, and bring forward whatever proofs are possible in support of my theories.

Perfect evolution in a Cuckoo's egg must mean that a degree of resemblance in colour, combined with size and shape, has been arrived at which is sufficient to ensure the continuation of the species in its proper numerical proportion with, or without, other controlling factors. There will, therefore, be no variation in such egg and comparatively little variation in the genera and species of birds selected as fosterers. Finally, such a state of evolution also infers that there is an ample supply of suitable fosterers laying eggs of the type to resemble which the Cuckoo's egg has been evolved.

No finer examples can be given of perfected evolution than the eggs of *Clamator jacobinus*, the Pied Crested Cuckoo, and *Hierococcyx varius*, the Common Hawk Cuckoo, the two most common

Cuckoos in India. These Cuckoos lay deep blue eggs which they deposit in the nests of birds of the genera *Argya* and *Turdoides*, two of the most common and universally distributed genera of birds in the Empire of India, which also lay similarly coloured eggs of about the same size and shape. Here we have two Cuckoos of different genera laying eggs so closely alike that it is practically impossible to separate them except by their size and the colour of the yolk. Even in size, however, they constantly overlap whilst, though the Hawk Cuckoo generally lays earlier in the year than does the Crested Cuckoo, in many places both birds are laying simultaneously. The genera *Argya* and *Turdoides* both lay unicoloured blue eggs, very glossy, hard-shelled and broad, blunt ovals in shape. The Cuckoos both lay eggs very similar in colour but with a softer, more satiny surface, less glossy and with much thicker shells. In shape they are more spherical or elliptical and in size generally a trifle larger than the eggs of *Turdoides* and much larger than those of *Argya*. In some instances both these eggs, as I have already said, are practically indistinguishable from those of the fosterer when lying side by side, though when being blown they are very easily distinguishable by the great thickness of the shells of the Cuckoos' eggs and by the colour of the yolks which are a much paler yellow, especially in the eggs of *Clamator*.

In these instances we have all the factors which seem to be necessary to hasten evolution. In the first place we have as suitable foster-parents two nearly allied genera containing numerous species of birds which are very numerous from the level of the plains up to about 4000 feet over practically the whole of India, Burma, and Ceylon. In addition to this, their breeding-season is very protracted and they are excellent mothers and fathers. Finally, they are very clever birds, and possibly elimination of dissimilar eggs would proceed with these fosterers faster than with most.

Another and almost exactly similar instance of perfect evolution is that of *Clamator coromandus*, the Red-winged Crested Cuckoo. This bird has a different breeding range to that of the last two, and is found from the foothills of the Eastern Himalayas, throughout the hills of Burma up to about 5000 feet, but it is most common as a breeding species at 1000 to 2000 feet. The most common birds within this area are the Laughing Thrushes of the family *Timaliidae*. Amongst these the genera *Dryonastes* and *Garrulax* contain the most numerous and most widely spread species and amongst these again the two species *Garrulax moniliger* and *G. pectoralis* are the two which are found throughout this great extent of country in the greatest numbers. These two birds, which are outwardly extremely alike, are the ones we should expect to find acting as fosterer to the Red-winged Crested Cuckoo, and so it is. These two Laughing Thrushes both lay pale blue eggs, and the Cuckoo lays an egg exactly similar in colour and about the same in size but differing not only in

texture but also in shape for, whereas the Laughing Thrushes normally lay rather long, oval-shaped eggs, this Cuckoo lays the most spherical of all eggs in the family.

This is rather interesting, for we find that not only is a spherical egg a very common form in reptiles, but that the more primitive non-parasitic Cuckoos also often lay spherical eggs. It would rather seem, therefore, as if shape was not a characteristic of much importance in birds' eyes, a theory which is confirmed by the difference in shape obtaining between other Cuckoos' eggs and those of their fosterers. Probably we may take this as a case of "complete evolution" if not of "perfect evolution," as all that is necessary has been achieved by the production of an egg similar in size and colour to that of the fosterer.

Yet another instance of complete, though not perhaps perfect, evolution may be found in the eggs of the Koel, *Eudynamis scolopaceus*, which lays its eggs in the nest of various species of the *Corvidæ*. Here we have birds, looked upon as the most astute of all the Passerine birds, regularly duped by a *smaller* bird, although everyone who knows India and who has taken the most superficial interest in birds, is fully aware that the Crow, whatever his species or race, has the bitterest instinctive hatred of the Koel.

The Koel is a large bird, and really belongs to a section of the Cuckoo family, the other members of which are non-parasitic. She naturally requires fosterers who are in a position to obtain a very large quantity of animal food for the voracious youngsters and, probably, in the area she occupies, the Crow is the only bird found from Ceylon to the Malay Archipelago whose habitat is as widespread as her own and who could furnish such food.

Accordingly we find that an egg has been evolved by the process of elimination sufficiently perfect for the purpose of hoodwinking the Crows and ensuring perpetuation of the Cuckoo. Crows' eggs are too well known to need much description but, roughly, they are pale bluish in ground-colour, with profuse blotching of dull red all over their surface, the general effect of the colour-scheme being a dark greenish egg. The Cuckoo's egg has been improved and perfected, until we get a type very similar in general colour to that of a Crow's egg but it is not alike in shape, for it is generally a shorter, blunter oval and in size it is much smaller.

The above three examples may all be said to be instances of *complete* evolution but I purposely use the term *perfect* evolution only in reference to the first two birds' eggs (*C. jacobinus* and *H. varius*). Here we have eggs so close to those of their foster-parent in colour, shape and size that often human eyesight is not acute enough to distinguish between the two. In the second case, the eggs of the Red-winged Crested Cuckoo and those of the Laughing Thrushes are very alike in colour and also in bulk, though their shape betrays them at once to the human

eye. In the third case, although we have an excellent and apparently sufficient simulation of the colour of the Crow's egg by the Koel's egg, yet any child could tell the difference between the two.

After reading the above, it will doubtless be asked whether the Cuckoos referred to do not ever deposit their eggs in birds' nests other than their normal fosterers.

As regards the first two birds, *H. varius* and *C. jacobinus*, certainly one hundred eggs will be found in the nests of *Argya* and *Turdoides* to every one in any other bird's nest.

Clamator coromandus lays at least ten times in the nests of *G. pectoralis* or *G. moniliger* to every once in other birds' nests and even then she generally deposits her egg in the nest of some other *Garrulax*, *Dryonastes*, or *Trochalopterum*, which are very closely allied birds and which lay eggs either very much like, or rather like, those of the proper fosterers.

The Koel may be said *never* to lay in any nest but in that of the true Crows. The only exceptions to the many thousands of eggs recorded are a few *deposited* in the nests of Magpies in Northern Burma and West China and one instance of its being laid in a Myna's (*Acridotheres tristis*) nest.

We may say, therefore, in the three examples given, the first including two species of Cuckoo, we have eggs which have arrived at a point in their evolution which is perfect or complete. Even if not perfect in human eyes, the adaptation in resemblance between the eggs of the Cuckoo and foster-parent is so great that a single type of the latter suffices over the whole range of the former to ensure a sufficient number of young Cuckoos being annually reared to replace normal loss. Further, the resemblance is sufficiently perfect to ensure deception of the fosterers without there being any necessity for variation in the Cuckoo's egg.

The above may, I think, be taken also as examples of wholly stabilized evolution, but it is perhaps advisable to explain that even this stability varies somewhat in degree. Thus in the eggs of both the Crested Cuckoos and in *Hierococcys varius* the colour is always the same and varies only very slightly in depth of tint. In the Koel, however, the variation is greater and, in fact, in this respect it may even be an advance in evolution over those of the others, for the variation in tint of colour, of extent of marking, etc., may all be evolved in order to give the possessor a better chance of escaping rejection.

All Crows' eggs vary greatly in colour; some are pale, some dark; some greener, some browner; in some the reddish markings predominate, in others they are almost absent. To suit such variation in colour there are two possible types of evolution which would occur to us as most useful: first, the production of an average coloured egg which would agree with an average number of Crows' eggs; secondly, a similar variation in degree of coloration in both Crows' and Cuckoos' eggs, so that an average number of eggs would match. The latter scheme is the

one which has prevailed and its value is curiously increased when we find, as we do, that in certain areas both Crows' and Koels' eggs show a certain tendency to a certain type, or degree of colour intensity. Thus the eggs of both Crows and Cuckoos in Assam eastwards average dark; those from the dry areas of Northern India average paler, whilst those from the dry desert areas of Sind, etc., are palest of all. Then when we come to Ceylon and the wet coasts of Malabar and Travancore, we again come back to dark eggs, whilst the drier regions of Ceylon seem to have a special reddish type confined to that island.

There are, of course, many more similar instances of perfect or complete evolution. For instance, there is *Clumator glandarius* in Spain and other parts of Europe which deposits its egg in the nests of Magpies but the examples given are sufficient, I hope, to prove that in some cases certain species of Cuckoos always lay the same type of egg and, normally, always cuckold the same species of foster-parents.

There is, however, another form of complete evolution which is even more interesting than the last and this is dimorphic evolution, or even, if I may use such a word, polymorphic evolution.

There are some species of Cuckoo which cover a far wider range of country than is covered by any one possible fosterer, and in some instances of this nature we find in their eggs the most wonderful contrasting examples of evolution.

The two most striking instances of dimorphic evolution known to me are to be found in the eggs of the two Cuckoos, *Cuculus poliocephalus* and *Hierococcyx sparveroides*.

Cuculus poliocephalus is a small Cuckoo which ranges from the Western Himalayas through the mountains of China to Japan. Over much of her western area she deposits her eggs in the nests of several of the small warblers of the genera *Phylloscopus* and *Acanthopneuste*. All these little birds lay either pure white eggs or eggs which are white, sparsely spotted. Moreover, she more often selects as fosterers those species which lay pure white eggs rather than those which lay spotted ones and her favourites seem to be *Acanthopneuste occipitalis* and *A. magnirostris*. With these fosterers a white egg is laid.

In Japan *C. poliocephalus* is as common as she is in the Himalayas, but here she selects as fosterer the equally common little *Cettia cantans*, a species which lays a remarkably beautiful deep terra-cotta or chocolate-pink egg. She seems to deposit her eggs almost invariably in this bird's nest and, accordingly, the egg she lays is similarly coloured, matching extremely well the fosterer's egg in everything but size. I believe the Rev. F. C. R. Jourdain has received specimens of this Cuckoo's eggs with other fosterers but he informs me that these eggs were taken by a Japanese collector about whom we know little and the late Alan Owston, who sent me over 30 of this Cuckoo's eggs, said he had never known it lay in anything but nests of *Cettia*. Throughout the

Chinese Hills I have little evidence of a sufficiently reliable nature for me to say what kind of egg the bird lays, but what little there is would lead one to suppose it to be the same as the Japanese form. In Eastern India our evidence is ample and here we find that the two types overlap so that from Assam to Garhwal we get both the pure white and the chocolate type but the first is the common one to the West, the second the more common in the East. In India, however, we have no true *Cettia* and accordingly we find that the normal fosterers in this country for the red eggs are the various species of the genus *Horornis*, all of which lay dark chocolate eggs which go well with the dark form of Cuckoo's egg. Other nests in which the Himalayan Cuckoo deposits her terra-cotta eggs are those of *Tesia* and *Oligura*, both genera (if they are divisible from one another) of birds which lay pink eggs not contrasting greatly with those of the Cuckoo.

It is true that with this last Cuckoo we have a great many instances of both red and white eggs being placed in nests containing eggs which are quite unlike their normal fosterers but this is what occurs more or less with every Cuckoo. It occurs least of all with those Cuckoos in which evolution has proceeded farthest, most with those Cuckoos in which the destruction of the unfit has only just commenced to operate. In the present case, however, neither of these factors can be considered alone. Here we have a bird, the eggs of which in each extreme of its habitat have by the process of elimination arrived at one definite type, which is in every way complete in so far as its local needs are concerned, whilst in the neutral country between the two extremes we have both types of eggs laid and consequently we obtain frequent instances of mistaken depositing. Eggs so deposited are probably not hatched in many instances and we shall thus, by the gradual elimination of the unfit, finally get two definite types of egg laid by the same species of bird within the same area, but always normally placed in its proper type of foster-parents' nest.

The next example of Cuckoo shows a further advance in this direction. *Hierococcyx sparveroides* lays two types of egg which contrast quite as strongly in colour as do those of *Cuculus poliocephalus* and we here also have a coincident variation in the size of the Cuckoos' eggs.

This bird, the Large Hawk Cuckoo, lays two types of eggs. The first is a dark olive-brown egg, varying somewhat in depth of colour and in the degree of olive tint. The surface is hard and glossy and the shape a very elegant, pointed oval. This egg is laid in the nest of the Great Spider-Hunter, *Arachnothera magna* and at least 20 eggs of the Cuckoo will be found in this bird's nest to one elsewhere and even of these latter the great majority will be taken in the nests of the Little Shortwing, *Heteroxenicus nipalensis*. The eggs of both the Spider-Hunter

and the Shortwing are very like those of the Cuckoo, the former more especially.

The second type of egg is a bright pale blue, similar in other respects to the brown egg, but much bigger. This egg is deposited in the nests of the Laughing Thrushes which lay eggs of a similar, sometimes almost indistinguishable, type to those of the Hawk Cuckoo. Another favourite fosterer is the Whistling Thrush, *Myiophoneus h. temminckii*, which lays eggs very like pale, washed-out specimens of those of blackbirds.

Now the blue eggs are laid by this Hawk Cuckoo all over its range in the Himalayas from the North-West, where they were taken by Col. Rattray, A. E. Osmaston, and others, right away to the Burmese Hills, where a great number have been taken by Messrs. K. Macdonald, J. M. D. Mackenzie, C. Hopwood, P. Wickham, and others. The brown type, on the other hand, appears to occur only in Assam, and even there practically only in the hills south and east of the Brahmaputra. The reason, however, does not require much searching for, as it is only in this tract of country that the Spider-Hunter occurs in sufficiently large numbers to ensure a constant supply of fosterers. Even in Assam, however, the blue-egg laying Cuckoo is almost as common as the other, so that here we get about an equal number of both eggs. There is, in spite of this, no intermediate form of egg in this area, nor do we ever find a blue egg in a Spider-Hunter's nest or a brown egg in that of a Laughing Thrush.

The last two examples are, as I have already pointed out, not quite parallel. *C. poliocephalus* lays two contrasting types of egg. In each extreme of its habitat only one form is laid, agreeing closely with the one type of fosterer selected but in the centre of this Cuckoo's habitat the two types of egg occur in equal numbers and the process of elimination has not yet arrived at a point where it has succeeded in wiping out all individuals which lay their eggs in wrong nests. *H. sparveroides* has advanced a stage further; it also lays two strongly contrasting types of egg, but it lays one type of egg which is blue from extreme east to extreme west of its habitat, whilst in one comparatively small district, only some 700 miles long, it lays a second brown type of egg which has been evolved to suit exclusively one particular fosterer, which is sufficiently numerous and, presumably, exceptionally suitable in other respects.

In both the above examples evolution seems to have advanced to a stage of completion or stability in regard to coloration and size of egg but in the one, *C. poliocephalus*, there still remains a complete degree of stability to be acquired in the selection of fosterers over a portion of the area inhabited. I should, however, say that, even in this instance, I personally place little importance on the fact that numerous eggs are laid in the nests of more or less abnormal fosterers, as this can be accounted for in many rational ways. This point I deal with more fully later on.

Turning now to instances of evolution which are incomplete but which show considerable advance, there can be no better example than that of the little Cuckoo, *Cacomantis passerinus*. This Cuckoo is found in different geographical races from Ceylon, through practically the whole of the Indian Empire. In many portions of its area we do not yet know what are its normal fosterers or we have not yet sufficient evidence to show to what degree evolution has progressed. We may say, however, that over most of its range it lays principally in the nests of *Cisticola*, *Orthotomus* and *Franklinia*; in the Nilgiris and adjoining hills it breeds freely, making use of the nest of *Prinia inornata*; in Assam and the North-East, where it is possibly more common than anywhere else, the fosterers selected are of the genera *Suya* and *Cisticola*; whilst in Hyderabad (Deccan) *Prinia socialis* seems to form the sole fosterer.

Has anything been evolved towards perfecting the resemblance of the eggs of *Cacomantis* to those of its many fosterers? The answer is "Yes, much"; and if we take them seriatim as given above, we shall find that this is so.

Roughly speaking, the eggs of *Cisticola*, *Orthotomus* and *Franklinia* are either white or pale blue in ground-colour and are speckled with dark brown in the first-named; blotched, spotted, or speckled with various shades of red or brown in the second and third. *Orthotomus* is the most common of the three genera and also the most universally distributed and with the longest breeding-season. *Cacomantis* over all this area lays an egg very like that of *Orthotomus* and not strikingly unlike that of the two other genera. The ground-colour varies from white to blue just as it does in the fosterer's eggs but the blotches are generally larger, paler and more smudgy in character than in any of the other eggs except those of *Orthotomus* and they are also decidedly larger.

In the Nilgiris the Cuckoos' eggs seem always to be pale blue with blotches of reddish, whilst those of its local fosterer, *Prinia inornata*, are blue with dark, bold blotches of reddish black or blood-red.

In Assam the fosterers selected, *Suya* and *Cisticola*, lay, the former, eggs which are white to rather deep blue-green, marked in many ways with specks, spots, and small blotches of reddish to blackish brown, the latter, white or very pale blue eggs speckled with brown. Of the two fosterers, birds of the genus *Suya* are the more popular, both *khassiana* and *crinigera* being impartially cuckolded.

Many of the Cuckoos' eggs agree fairly well with the eggs of *Cisticola* but many cannot, unless one tests the shell and weighs the egg, be distinguished from those of the other foster-parents of the genus *Suya*. I have seen as many as fifty eggs of these birds in one season in the Khasia Hills, but I am quite sure that many of these would have escaped my notice had I not been always on the look-out for Cuckoos' eggs and naturally suspicious

of any egg in the least differing from the others. Once suspicion was aroused and one knew the differences to expect, it was, of course, very easy to say whether or not the egg was that of a Cuckoo. The differences are those to which I have already referred, viz., a very stout, heavy shell of rather coarse texture, a feebly coloured yolk and a weight far greater than that of similarly sized eggs of the foster-parent.

Mr. C. F. M. Swynnerton has already referred to the question of polymorphic colouring of the eggs of Cuckoos (Ibis, 1918, p. 127) and also of the foster-parents, and I also have commented on it (Ibis, 1913, p. 384).

When we come to Hyderabad we find the most extraordinary case of nearly completed evolution which I know of in the whole history of Cuckoos' eggs. The bird selected as fosterer within a very small area only a few miles across, round about this city, is little *Prinia socialis*, a bird which lays a bright red egg, utterly unlike the eggs of any of the other fosterers. Yet we find within this tiny area, where the Cuckoo is very common, a red egg has been evolved in order to ensure the preservation of the species. Why *Prinia socialis* should have been selected as a foster-parent is not very obvious, for though it is extremely common in Hyderabad, breeding in every garden and hedge, yet *Orthotomus* also is not rare and one would have thought would have sufficed. Evidently, however, *Prinia socialis* is the better foster-parent for local needs as it has completely ousted the Tailor-Bird within Hyderabad, though only a few miles away from the city the former bird is deserted and the latter again imposed upon.

It would seem that this evolution of a red egg is comparatively modern, as it has not reached the stability of any of the eggs which I have cited as examples of complete evolution. The original discoverer of this red egg was Professor K. Burnett of the Hyderabad College, to whom I owe a beautiful series, others being taken by Col. R. Sparrow, Sergt. F. Kemp, etc. Professor Burnett having found two red eggs took one and sent it to me. The second was hatched and the bird, when fully fledged, also forwarded to me and its identity so made certain. In collecting a series, however, Professor Burnett found it much easier to get fully red eggs than such as were intermediate between them and the usual types of this Cuckoo's eggs. After many years constant work by Professor Burnett and a final most generous gift to me of his whole series, I have been able to link up the red eggs with the others, thus giving a most perfect demonstration of an egg in the course of evolution. Unfortunately these little eggs fade very rapidly, possibly *because* of their recent evolution, and neither plates, magic-lantern slides, nor the eggs themselves, give a proper idea of their beautiful colouring when fresh.

With this example before us it hardly seems necessary to labour further the question of whether Cuckoos' eggs are still undergoing some phase of evolution, but in discussing the

evolution of the eggs of our Common Cuckoo, *Cuculus canorus*, the point will repeatedly come up. *Cuculus canorus*, which may be taken as the type of Cuckoo in which evolution is most backward, is the Cuckoo with the greatest range of all Cuckoos, ranging practically throughout Europe and Asia as well as through much of Africa. The geographical races with which I am best acquainted are *C. c. canorus*, breeding in Europe, *C. c. telephonus*, breeding in Western and Northern Asia, and *C. c. bakeri*, breeding in the Eastern Himalayas, Burma and, probably, Western tropical China where the mountains are high enough, i. e. 5000 feet and over. The degree of evolution obtained varies greatly in the different geographical races and, moreover, it even varies greatly in individual strains in each race.

Taking first our English Cuckoo, *Cuculus canorus canorus*, we do not find that evolution has advanced very far. The common fosterers cuckolded by this bird are the Wagtail, *Motacilla alba*, the Robin, the Reed-Warbler, the Pipits, *Anthus pratensis* and *Anthus trivialis* and the Hedge-Sparrow. There is certainly no example of perfected evolution in England. If we take the Hedge-Accentor first, we find that there is no such thing as a blue Cuckoo's egg known in England, although one or two reputed eggs are in collections. The nearest approach to blue eggs is probably shown by the series collected by Mr. Owen round about Felsted, which are a rather pale blue-grey, sparsely spotted and blotched with darker. If we examine large series of eggs taken by genuine collectors with the three fosterers, Pipits, Wagtails, and Reed-Warblers, we find that the Cuckoos' eggs go very fairly well with all of them and also that the contrast is not very startling as between them and the Robin's eggs. This looks, therefore, as if evolution had arrived at a point at which an inconspicuous egg had been evolved which agrees comparatively well with the five normal fosterers, whilst in respect to the Hedge-Sparrow it would appear that this bird is so extremely foolish that little or no evolution has taken place, or indeed, is necessary.

A closer examination, however, of large series of eggs, although it shows no case of evolution such as is found in the eggs of the Cuckoos we have previously dealt with, does show signs of something taking place in the way of elimination of the unfit. In one hundred sets of each of the five fosterers named, I find that of those eggs placed in the nests of Wagtails, the majority are rather pale, whilst the general trend of those placed in the nests of Pipits and Reed-Warblers are rather dark. Amongst the eggs of Cuckoos found in Robins' nests there are certainly a greater percentage of eggs with a reddish tint, although pale ones do not, as we should expect, appear to be any more numerous than dark ones; finally, with the Hedge-Sparrow we find almost any type of egg, though even amongst these we get Mr. Owen's beautiful series of *rather* bluish eggs.

In England, unfortunately, a large proportion of the Cuckoos' eggs in collections have been supplied by dealers who, even if they would not cheat intentionally, are themselves deceived by the men who supply them, who are generally paid prices according to the rarity of the foster-parent with which they are supposed to have been taken. For this reason we have to dismiss from our calculations about two-thirds of the eggs in private collections. Outside the five best known fosterers, there are a few others well authenticated which we may accept as normal fosterers, such as the Sedge-Warbler, Spotted Flycatcher and one or two others. As regards the rest, I cannot consider them as anything but abnormal or casual. Dr. R. Williams, nearly forty years ago, showed how certain Cuckoos which normally cuckolded Wagtails, Robins, and Hedge-Sparrows, occasionally deposited their eggs in the nest of practically any other small bird building within the area they covered when they could not find a nest of the species they really wanted.

Perhaps no one in England has personally taken more Cuckoos' eggs than Dr. Williams, whom I found to be possessed of a wealth of knowledge on the subject. The greater number of his eggs were given by him to Dr. Rey but I was so fortunate as to obtain nearly 150 from him after he had ceased sending them to that gentleman. From these most interesting sets, I find that practically all the casual eggs laid in such nests as those of the Bullfinch, Linnet, Greenfinch, Wren, Chiff-Chaff, etc., can be matched with those of Cuckoos which year after year deposited their eggs in the nests of some one of the three birds which in his vicinity provided the normal fosterers.

Continental Cuckoos seem to have advanced considerably further in evolution than have the individuals which yearly seek our shores for breeding purposes. True, we cannot say that in any instance complete or perfect evolution has been arrived at but many instances show that elimination has already been very busy and thus certain fosterers have been accepted through sufficient generations to allow of all those Cuckoos who laid eggs in striking contrast to their own to be completely exterminated. Thus we find that the Cuckoos' eggs now placed in the nests of many birds such as the Great Reed-Warbler, the Red-backed Shrike and a few others, approach very closely both in colour and character to the eggs of their foster-parents. The degree of resemblance varies greatly, some eggs are an excellent match and some are only fair, whilst strongly contrasting eggs are in a very small minority and even these, of course, may have been deposited by Cuckoos normally cuckolding other fosterers.

Perhaps the greatest advance shown by Continental Cuckoos is the evolution of a blue egg to resemble those of the Redstart with which they are placed. This blue egg seems normally to be laid only by certain individuals which breed in the Baltic States and East Prussia, more especially in Finland. Even here, however, blue Cuckoos' eggs are not always placed with the blue Redstarts'

eggs and it would seem that whilst a few individual Cuckoos have reached a very high degree of evolution in this respect, the great majority are still only in its earliest stages.

Leaving the European Cuckoo and moving farther east into Asia, we find a very closely allied form, *Cuculus canorus telephonus*, apparently depositing eggs which are much further advanced in evolution. Unfortunately, we have not much material to work on but even among the few eggs I have seen of this bird—under two hundred—there appear to be many cases of advanced evolution. The most noticeable, perhaps, are to be found in the very close resemblance between the eggs of the Red-backed Shrike, *Lanius schach erythronotus*, the Spotted Forktail, *Enicurus maculatus maculatus* and the eggs of the Cuckoos which respectively victimize these two birds.

Again, we find that *Calliope* seems to form a favourite fosterer for this Cuckoo, and all the eggs placed in the nests of these birds have a very distinct blue ground also, one or two being but very faintly marked.

These eggs were all taken in the extreme North-West of India, but the farther east we work, the more advanced the evolution. In the Central Himalayas the two favourite fosterers seem to be *Trochalopteryx lineatum* and *Larvivora brunnea*, or, in certain areas, *Saxicola torquata indica* and *Oreicola ferrea*. The first two birds lay unicoloured bright blue eggs, the last two, bluish eggs very faintly marked with pale reddish. To go with these eggs we have a beautiful blue egg evolved and it is seldom one finds a Cuckoo's egg of any colour but blue placed in the nests of these birds. Working yet farther east we come to another race of Cuckoo, *Cuculus canorus bakeri*, a very sedentary bird, breeding at comparatively low levels and migrating for very short distances into the plains in winter.

As with the other races, so with this species, the number of fosterers cuckolded is very large, and we have no signs that evolution has been in existence long enough to eliminate all but those Cuckoo individuals which deposit their eggs in only the nests of one, two, or a few of the birds which are the most suitable for the purpose of bringing up their young. We do, however, find that normally, the number of species called upon to rear the young Cuckoo is much more restricted than it is farther west. For example, in Assam, nineteen out of twenty eggs—perhaps a much greater percentage even than this—will be found in the nests of the two genera *Cisticola* and *Suya*, both consisting of small Warblers which swarm all over the hills above 4000 feet, or in the nests of Pipits. The *Cisticolas* are of two species, *C. c. curesitans*, extremely common, and *C. tytléri*, rather rare. The former lays a tiny white or bluish-white egg speckled or spotted with reddish brown; the latter lays a bright blue egg boldly spotted with very dark brown. The eggs of the *Suyas* vary much more, indeed they may be said to be polymorphic, for the ground colour may be white, pink, bluish, blue-

green or greyish pink and the character of the markings is almost as varied as the ground-colour. The most common type of egg undoubtedly has the ground white to pink or pinky-grey, the surface profusely covered with small spots and specks of reddish brown. Now evolution has produced for this Cuckoo in Assam, eggs which vary from pure white with numerous small specks of reddish, to deep pink heavily marked throughout with various shades of reddish brown. The first type is generally placed in the nests of *Cisticola* and agrees with the eggs of that bird in all respects but size; the second type of egg is most often deposited in the nest of *Suya* and agrees well with the most common red type of that bird's egg.

As regards the Pipits, two species are called upon to do duty, the first, *Anthus richardi striolatus*, a very rare bird which breeds on one or two ridges only, and *Anthus richardi rufulus* which breeds in considerable numbers up to about 5000 feet or a little higher. Here the only signs of evolution traceable are in the fact that the majority of Cuckoos' eggs deposited in these nests are dark and therefore do not contrast strongly with those of the Pipit.

With *C. c. bakeri*, blue eggs are much less common than they are with *C. c. telephonus*, doubtless because suitable fosterers laying blue eggs are not available. We, however, do find such eggs occasionally, and these most often in the nests of either *Liothrix lutea* or *Mesia argentauris*, birds which lay bright blue eggs marked boldly with reddish brown or purple-black. In these cases, too, we often find that the blue Cuckoos' eggs are more or less spotted. It would be possible to continue instances of incipient and partial evolution in the eggs of *Cuculus canorus* and its geographical races almost *ad infinitum*, but perhaps more than enough has been written to prove beyond all doubt that the three degrees of evolution taken as a basis for this article do exist.

From Australia I have not been able to obtain any material to help me much in my work. This has been because, as in England, collectors vie with one another not in getting eggs to prove some theory or to form a basis for another but in getting eggs with a great variety of fosterer. Future work by Messrs. Orton, Berthling, Archer, and others should prove of great assistance and value and material should be available before long sufficient to enable us to decide what is happening in Australia.

I have not commented on many other Cuckoos, the eggs of which are fairly well known, such as various species of *Chalcococcyx*, *Hierococcyx nigricolor* and *fugax*, *Penthoceryx sonnerati*, *Surniculus*, etc., etc., as though none of these afford any evidence contradicting what I have written, yet none of them afford such good instances of the various stages of evolution as those I have selected for the purpose.

Perhaps, before leaving the subject of Cuckoos and their eggs,

I may be permitted briefly to refer to the method adopted by Cuckoos for placing their eggs in the nests of other birds. Mr. Chance has proved that sometimes at least, *C. canorus* lays her eggs direct into the nests of Pipits, whilst Mr. Scobey has almost equally well proved that she does not always do so in the nests of Wagtails but deposits them therein with her bill.

Now in India, *Hierococcyx sparveroides* could certainly never get inside a nest of *Arachnothera magna*, not only because it is too small, but the shape of the nest prevents it. On the only occasion on which I have personally taken an egg of this Cuckoo from this bird's nest and also seen the Cuckoo at it, all the latter did was to cling desperately for a second or so to the outside of the nest, or to the stalk of the leaf beside it, whilst the parent Spider-Hunters ineffectively hustled her. Certainly, I cannot say I saw her place the egg inside the nest with her bill but, equally certainly, she did not get inside it, yet the egg was there when I arrived. Again, I have seen, and others have seen, *Clamator jacobinus* deposit her egg in the nest of *Argya* with her bill, though it is probable that both *C. jacobinus* and *C. coromandus* do, not infrequently, lay direct into the nests of these genera.

Cuculus c. bakeri lays the great majority of her eggs in the nests of *Cisticola* and *Suya*, both genera which build tiny egg-shaped nests of grass far too small to contain the Cuckoo chick when half grown, much less large enough to allow a Cuckoo to sit in them. I have seen very many hundreds of these little birds' nests with Cuckoos' eggs in them and it was obvious from their perfect condition that no attempt had been made by the Cuckoo to get inside them. When the young Cuckoo hatches and commences to grow, the grass-work of the nests expands so as to form a trellis-work round it until finally it bursts and the young Cuckoo either falls to the ground or remains perched on a pad of broken-down nest. But Cuckoos' eggs have been taken from nests even more impossible of access than these grass nests. Thus Mr. J. Livesey and Capt. Bates found a Cuckoo's egg in the nest of a *Phylloscopus* built in a hole in a tree, the entrance to which was only big enough for the tiny warblers to go in and out. The nest was some way in and the Cuckoo's egg in rolling in had smashed one of the eggs of the owner in falling. Twice I have taken eggs of *Cuculus c. bakeri* from hollow bamboos in which an *Abrornis* had built its nest and in neither of these cases could the old Cuckoo have got more than its head into the hole, whilst the young Cuckoo, if hatched, could certainly never have got out. Col. R. H. Rattray found an egg of *C. c. telephonus* in Danga Gali, near Murree, placed in the nest of *Acanthopneuste occipitalis*. This nest was in amongst the roots of a tree and the Cuckoo had had a desperate struggle to get even its head to the nest, losing many neck feathers in its final struggle to overcome the last inch or two. Messrs. Inglis & Primrose took several eggs of *Chalcococcyx* from the nests of *Ethopyga seheria* and in no case were any of these tiny fragile nests

injured in any way, as they must have been had the Cuckoo tried to force an entry into them. Yet again, Mr. W. E. Wait found a young *Surniculus* in the nest of a *Rhopocichla nigrifrons* in Ceylon, and this young bird, though not half-grown, completely filled the nest, into which no full-grown bird could possibly have crept.

I understand that Mr. Chance suggests that even when Cuckoos do not enter nests for the purpose of laying their eggs, they place themselves in such a position that they can shoot the eggs by natural means into the nest direct from the oviduct but this suggestion may be negatived from the fact that Cuckoos very seldom smash the eggs of the tiny foster-parents with their own heavy eggs, which would assuredly be the result if they adopted such a method. Moreover, many nests are so placed that no Cuckoo could obtain a foothold which would enable her to assume a position suitable for such an action; whilst many other nests are so fragile that they would never stand the weight of an adult Cuckoo hanging on to them during her acrobatic performances.

I have dealt in this paper with only one aspect of Evolution in regard to Cuckoos and their eggs but this subject opens out a very wide field for observation. Thus certain recent theories of "age and area" are certainly not confirmed by a study of the distribution of the *Cuculidae*. Again, many of the tenets of Mendelism and the heredity of acquired characteristics seem to be contradicted by the evolution of Cuckoos' eggs. But these are big subjects and I merely refer to them here to show how great an asset a wisely acquired collection of eggs may be in the study of evolution and connected sciences.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. *Clamator jacobinus*. An oviduct egg.
 3. " " Ex nest of *Turdoides terricolor*.
 2. *Turdoides terricolor*.
 4. *Argya caudata*.
 5. *Turdoides griseus striatus*. } Common fosterers to *C. jacobinus* and *H. varius*.
 6. *Argya subrufa*. }
 7. *Hierococcyx varius*. An oviduct egg.
 8. *Clamator coromandus*. Ex nest of *Garrulax moniliger*.
 9. *Hierococcyx varius*. Ex nest of *Argya caudata*.
 10. *Grammatoptila striata*. Common fosterer in extreme N.W. Range.
 11. *Garrulax moniliger*. } The two most common fosterers to *C. coromandus*.
 12. " *pectoralis*. }

PLATE II.

- Fig. 1. *Corvus coronoides culminatus*. (Siam.)
 3. *Eudynamis scolopaceus*. From nest of 1.
 2. *Corvus splendens insolens*. (Burma.)
 4. *Eudynamis scolopaceus*. From nest of 2.
 5. " " From nest of 7.
 7. *Corvus splendens splendens*. (Behar, N. India.)
 6. *Corvus splendens protegatus*. (Ceylon.)
 8. *Eudynamis scolopaceus*. From nest of 6.
 9. *Corvus coronoides intermedius*. (Assam.)
 10. *Eudynamis scolopaceus*. From nest of 9.

PLATE III.

- Fig. 1. *Cuculus poliocephalus*. White type from nest of 2.
 2. *Acanthopneuste occipitalis*.
 3. *Cuculus poliocephalus*. White type from nest of 4.
 4. *Phylloscopus affinis*.
 5. *Cuculus poliocephalus*. Red type from nest of *Cettia cantans*.
 6. *Cettia cantans*. (Japan.)
 7. *Cuculus poliocephalus*. From nest of *Horornis fortipes*.
 8. *Horornis fortipes*. (Assam.)
 9 to 11. *Hierococcyx sparveroides*. Brown type from nests of *Arachnothera magna*.
 12 to 15. *Arachnothera magna*. (Assam.)
 16 to 18. *Hierococcyx sparveroides*. Blue type from nests of *Garrulax moniliger* and *Lanthocincla cineracea*.
 19. *Lanthocincla cineracea*. (Burma.)

PLATE IV.

- Figs. 1 to 4. *Cacomantis merulinus*. Blue types from nests of 5 to 9.
 5, 6. *Orthotomus sutorius*.
 7. *Franklinia gracilis*.
 8, 9. *Suya crinigera*.
 10 to 14. *Cacomantis merulinus*. White types from nests of 15 to 19.
 15, 16. *Orthotomus sutorius*.
 17, 18. *Suya crinigera*.
 19. *Cisticola cursorians*.
 20 to 23. } *Cacomantis merulinus*. Pink types ranging from the least to the
 25 to 27. } best developed type, all from nests of *Prinia socialis*.
 24 & 28. *Prinia socialis*.

21. A Comparative Study of the Buccal Glands and Teeth of the Opisthoglypha, and a Discussion on the Evolution of the Order from Aglypha *. By SUSHIL CH. SARKAR, F.Z.S.

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(Text-figures 1-29.)

Introduction.

The comparative anatomy of the buccal glands, teeth, and the problem of the evolution of the opisthoglyphous Snakes forms the subject of this paper, and was suggested to me by Professor G. E. Nicholls, under whose supervision the investigation was begun in the Biological Department of King's College for Women, Household and Social Science Department. After the research had been in progress for three months Dr. Nicholls had to leave for Australia, and since then the work has been carried on under Miss Philippa C. Esdaile, D.Sc., F.Z.S. It is with pleasure that I acknowledge my indebtedness to Dr. Esdaile for her invaluable advice and criticism during the progress of the work.

I wish also to express my obligation to Professor Dendy and the Government Grant Committee of the Royal Society of London for a grant-in-aid. Lastly, I have to thank Miss Alfreda Newton for her kind assistance in cutting series of sections of a large number of heads of snakes, and also for taking photographs of specimens and sections.

Historical Facts.

The snakes chosen as types in this research belong to the Aglypha and Opisthoglypha, *i. e.* two of the three divisions of the Family Colubridæ. These differ from one another by the fact that in the Aglypha all the teeth in the maxilla are solid, whilst in the Opisthoglypha one or more grooved teeth are present in the posterior region. The members of the latter group are more or less poisonous.

The group Opisthoglypha is of special interest in that it is considered to be the connecting-link between the Aglypha on the one hand and the Viperidæ (with grooved teeth at the anterior end of the jaw) on the other; the group Proteroglypha is believed to have developed independently and directly from the former. Although the possible evolution of the Opisthoglypha was pointed out by Boulenger, no research to verify his statements has been attempted in connection with the important

* Thesis submitted for Ph.D. degree, University of London, June 1922.

organs, such as the poison gland, its duct and poison fangs, taken concurrently. So far as I am aware, this is the first research on these lines.

The presence of grooved teeth in the posterior region of the maxilla was first observed and discussed by Thomas Smith (11) and later by J. G. Fischer. In the year 1892, Niemann (6) published an account of the structure and relationships of the glands of the upper lip in general, but he described only three types of the Opisthoglypha. His work on this group is very scanty, while the diagrams are insufficient and wanting in detail, but the connection of the duct and the groove of the fang is well emphasized. In 1895, West (15) published a detailed description of the buccal glands and teeth of opisthoglyphous snakes. His paper made a considerable advance in the knowledge of this subject; his observations are still looked upon as a good groundwork, and his work is quoted by various authors. His descriptions, however, relate only to morphology. I have described four more genera of this group—*Chrysopelea*, *Tarbophis*, *Psammophis*, and *Cerberus*; the first two were not mentioned at all by West, and of the other two he gave only a short description of the teeth.

It was in 1896 that Boulenger put forward an account of the probable evolution of the Opisthoglypha from the Aglypha. He pointed out that in the higher genera of the Aglypha the series of teeth in the jaw shows an increase in size from in front backwards, so that we are gradually introduced to the opisthoglyphous condition, with a large fang in the posterior region of the jaw. In the higher types of both the Opisthoglypha and Proteroglypha this fang is always distinctly bigger than the tooth in front of it. Therefore in my discussions of the probable evolution of the fang of the Opisthoglypha from the somewhat enlarged posterior tooth of the Aglypha, I have selected those snakes in the Aglypha in which the posterior tooth is clearly larger than the preceding one—e. g., *Tropidonotus* and *Lycodon*.

Among recent papers on the Ophidia, those of Mary Phisalix are the most important. In her work (9) she discusses the accounts given by various authors, and she has attempted to arrange the members of this group in an ascending series on evolutionary lines, according to the disposition of the teeth. In this paper I have attempted a like task, but my series differs from hers in that I have tried to select for consideration only those Aglyphodont forms in which the last tooth has become markedly different from the rest. Also I have discussed what I consider to be the highest grade of evolution in the Aglypha—i. e., the condition presented by those types in which the last tooth has acquired two cutting-edges instead of only one. Mary Phisalix does not continue her series beyond those with one cutting-edge. It should be noticed that my diagram of *Tropidonotus stollatus* (text-fig. 10) differs from hers (see p. 164, ref. 9).

The hinder tooth in my diagram of this species is represented as larger than the one in front of it. My observation is gathered from the dissection of several specimens.

Methods and Material.

Most of the snakes used for my observation were brought from India by myself. Some of them were preserved specimens, well fixed and suitable for histological purposes.

Unfortunately others which I had hoped to keep alive for physiological experiments had to be killed unexpectedly, and the tissues were only imperfectly fixed.

This investigation has necessitated the preparation and examination of a number of serial sections of the heads of snakes, and owing to the presence of the scales and hard bones forming the skull, this proved to be a difficult task. After many experiments the following method was successful.

The head was separated from the body close to the angle of the jaw, and placed in the fixing and decalcifying reagent aceto-bichromate (Bolles Lee, pp. 49 & 50). In order to ensure thorough penetration of the fluid, an incision in the scales was made just behind the eye, the lens of which was also removed. After a fortnight the head was taken out, and was carefully cut by means of a sharp razor into two halves by a median longitudinal vertical cut. Each half was again placed in fresh aceto-bichromate solution with the addition of one or two drops per 100 cc. of acetic acid. I found it necessary to leave it in this for three to four weeks to get complete decalcification. Each of the halves was then used for longitudinal or transverse sections. It was found necessary to leave the head in the paraffin bath at a low temperature for more than twelve hours. The sections were cut at a thickness of 10-15 μ . Several stains were tried, and I found the following most useful: Ehrlich hæmatoxylin counter stained with eosin or hæmalum and eosin. Each of these methods gave a good differentiation between the serous and the mucous secreting cells in the poison gland, the former being stained pinkish, the latter bluish. Both these being water stains, I found that the teeth and bone were often washed off the slide while being taken through the alcohol. To prevent this the slides were dipped in a thin solution of colloidin in 90% alcohol. In order to verify my observations with regard to the duct and its connections with the fang, I made several cardboard models of portions of the jaw.

General Discussion on the Teeth in the Mandible and Maxilla and the Mechanism of the Hinged Teeth.

The maxilla, mandible, and pterygoid bear teeth and these occur in uninterrupted series, increasing or decreasing in size from in front backwards. Sometimes a diastema is left, and this is

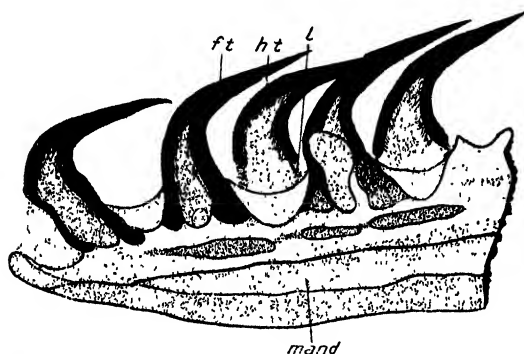
generally found in front of the tooth, which becomes bigger than the rest (*Dryophis*). The maxillary and mandibular teeth are mostly inclined posteriorly at a considerable angle—i.e., the proximal part of each tooth for a little distance is almost at right angles to the bone, while the distal part bends backwards. The teeth appear to be of various types when seen in transverse section—round, triangular, flattened, etc. But more interesting still is the fact that the alternate teeth are hinged and fixed. In the dried specimens the hinged teeth frequently drop out; the dropping-out of the teeth after death has been frequently noticed by several workers, including Boulenger, and was accounted for by the accidents of preparation.

Thus, quoting Boulenger:—

“It very often happens that every alternate tooth having dropped out, the jaw appears, on a superficial examination, to possess half the real number of teeth.”

At first, while making dissections of a large number of snakes, I often found that some of their teeth differed from the others

Text-figure 1.

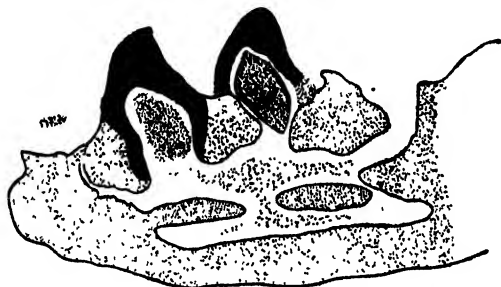


Tropidonotus stolatus. Portion of mandible seen in lateral view, drawn with camera lucida from a cleaned specimen. *ft.* fixed tooth; *ht.* hinged tooth; *l.* ligament; *mand.* mandible. $\times 40$.

in that they could be bent backwards. I took it to be that these teeth were being either gradually fixed or were about to drop out of the jaw. On a more careful examination, I found that these loose teeth, as a general rule, alternate with the fixed ones. This regularity led me to suspect that the condition was not accidental. In order to verify this, I examined a number of cleaned skulls, and found that these loose teeth either drop out, leaving spaces or remain somehow fixed to the jaw, so that it is difficult to distinguish them from the fixed ones. I concluded from this that there must be some ligament or structure which

keeps the tooth attached to the bone, but this hardens when dried, giving the tooth an appearance of being fixed. In order to make a further examination, I mounted the decalcified jaw complete, carefully dissected out from the head of the snake. In text-fig. 1 it will be seen that there are three fixed teeth, while the other two are attached to the socket by means of connective tissue (Z), and there is a space, one tooth having dropped out during the process of dissection. I also cut sections of the heads of different genera, taking care to cut the jaw as nearly longitudinally as possible. Externally these hinged teeth differ from the others by being bent more sharply, and also, when moved with a needle, they can be made to bend towards the median line. As regards the forward movement, it is limited to a certain extent. At the base also the two sets of teeth differ from one another by the fact that the hinged teeth have a whitish appearance, due to the presence of the connective tissue which holds it to the bone. In order to study the

Text-figure 2.

*Tropidonotus stolatus*. Longitudinal section of mandible with teeth. $\times 92$.

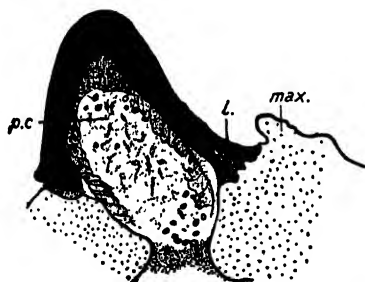
mechanism of its movement, I carefully examined the series of sections of the tooth and the bone. Text-fig. 3 shows a diagram drawn from a longitudinal section taken at about the middle of the tooth. It will be noticed that the facets in the maxilla at the base of the two ends of the tooth differ in their structure, and, at the same time, the base of the tooth differs markedly at the anterior and posterior ends. In the front the base ends in a peculiar, slightly knob-like structure which also projects inwards. This fact was also noticed by Tomes (13), who writes as follows:—

“As the tooth approaches completion, there is a peculiarity in the form which its base assumes and which I have not noticed in other animals, namely that the dentine at the widely open base of the tooth is often abruptly bent inwards as though the base of the tooth were about to be closed by a sort of operculum of dentine.”

In his plate Tomes has given figures of sections of four or five teeth, and he has shown the bending in one only, and this also at the anterior side. This evidently proves that this was one of those hinged teeth.

This knob-like structure at the anterior edge of the tooth fits into the slightly concave, vertically inclined, smooth facet of the bone, so that when the tooth is pressed forward it strikes against the slightly inclined plane and is prevented from further bending. At the posterior side the distance between the bone and the end of the tooth is greater. The connective tissue between these two structures is more prominent, and its histological structure can be examined. Under the high power it has the appearance as shown in text-figs. 3 and 4, and it resembles white fibrous tissue. It has not at all the appearance of developing bone or enamel. Had it been enamel it would have been dissolved by the continued action of the acid in the decalcifying

Text-figure 3.



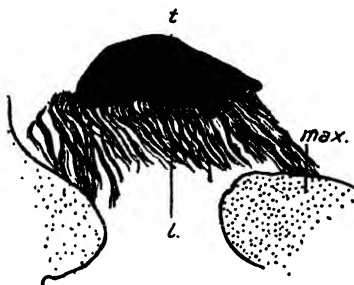
Tropidonotus stolatus. Longitudinal section of maxilla, showing a loose tooth with its connective-tissue attachment. *l.* ligament; *max.* maxilla; *p.c.* pulp cavity. $\times 260$.

solution, to which it was subjected for more than a month. Text-fig. 4 shows also the connection of the same tooth at the posterior edge. It will be noticed that the connective tissue (*l*) keeps it attached to the bone. Thus we see that the tooth when pressed from in front moves so that the hinder end of the base, which has a greater field in which to move, is pressed down on to the bone; but it is prevented from slipping further by the connective tissue; while, on the other hand, if the tooth is pressed forwards from behind, its power of movement is restricted by the inclined edge of the socket of the bone and also by the band of connective tissue at the hinder end, which, so far as can be ascertained at present, appears to be non-elastic. This hinged and fixed arrangement I have found to be extended to the grooved teeth. If there are two grooved teeth, one of them is hinged and the other fixed. It depends upon the arrangement of the other teeth whether the anterior or the

posterior one is hinged. It often happens that either the two or three consecutive teeth drop out from the dried bones. This is due to the fact that one of the fixed teeth is being replaced.

The function of such an arrangement is difficult to determine, but it seems to provide a firmer grip for the prey. While the prey is being taken into the mouth and forced towards the gullet, these hinged teeth, which point inward and backward, bend down; so that when the prey is struggling to escape from the mouth, the teeth, being hinged, allow it to pass downwards into the gullet but not outwards. Therefore from these observations I am led to conclude that the hinged teeth are not part of a series in the course of development which will become ankylosed to the jaw, but that they will always remain hinged, and during life will be held in place by the band of connective tissue, while after death they may drop out. This opinion is further emphasized by the facts that: firstly, in the maxillæ and

Text-figure 4.



Tropidonotus stolatus. Longitudinal section of maxilla, showing a loose tooth with its connective-tissue attachment. *l.* ligament; *m.* maxilla; *t.* tooth. $\times 260$.

mandibles of the dried skull of the adult we can clearly see the plane facets at the anterior end of the sockets, which show that it has been subjected to constant friction; secondly, if the tooth were to be later ankylosed to the jaw-bone, there would be no necessity for the inbending of the anterior end of its base; thirdly, it is inconceivable that in the numerous cases I have examined, every second tooth should become worn out or drop out accidentally.

The grooved fangs are always placed at the posterior end of the maxilla. Sometimes they are situated far back in the mouth, so that their points are quite hidden within the angle of the jaw. In this case the teeth are considerably bent (*Dipsas*), but where they are a little more forward in the mouth they are generally straighter. In shape they may be either flattened (*Oxybelis*) or circular (*Psammophis*), or may have a cutting-edge developed at the posterior region. The grooves are either placed in the

front face of the tooth or on the external surface. In some cases the groove slightly curves round in its course; it may extend throughout the length of the tooth or may end a little above the tip. The groove may be shallow, or may be widely open or almost closed.

*Morphological Description of the Dissection of the Heads
of a few Opisthoglyphous Snakes.*

Genus DRYOPHIS.

DRYOPHIS MYCTERIZANS. (Text-fig. 19.)

The poison gland is distinctly definable from the superior labial gland, and is large and extends a little further forward than the middle of the eye and posteriorly a little behind the angle of the jaw. The superior labial gland reaches to the anterior extremity of the maxilla, and it extends a little behind the poison gland. The two portions of the gland are continuous with one another. Near the region of the fang-like tooth in front the gland becomes broader. The inferior labial gland consists of a very thin strip of glandular tissue, and does not extend as far as the angle of the jaw. There are fourteen teeth altogether in the maxilla, and they are arranged as follows:—four small teeth in front, then two large fang-like teeth, followed by a diastema, then six very small teeth, and finally two very large, stout, and straight grooved teeth. The groove is on the outer side and is deep and extends throughout the length of the tooth. The duct of the poison gland opens near the base of the tooth. There are eighteen teeth in the mandible. The first is rather small, the next three very large, the middle of the three being the largest, then a diastema, which is followed by fourteen teeth which gradually diminish in size. The Harlerian gland is much reduced, and consists of a thin strip of tissue lying behind the eyes in the eye-socket.

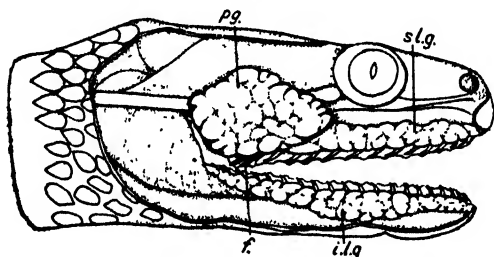
Genus CERBERUS.

CERBERUS RHYNCHOPS.

The poison gland is clearly distinguished from the upper labial gland, and is large and oval (text-fig. 5); it is so distinct an organ that it can be easily picked up from the surface of the superior labial gland without injury to the latter. The superior labial gland extends from the anterior end of the maxilla and posteriorly up to the poison gland. Practically the whole of the posterior portion of the glandular area is occupied by the poison gland, so that the superior labial gland does not extend far behind the eye. The lower labial gland also does not extend up to the angle of the jaw; this is probably due to the sharp upward turning which the lower jaw takes, thus giving a greater

extension to the mouth and placing the fangs in a more exposed position. There are eighteen maxillary teeth; the last two are grooved and large. The grooved teeth are placed slightly further forward away from the angle of the jaw. The hinder grooved tooth is hinged. The groove is situated on the anterior side of the tooth at its proximal end, while on the outer side at the distal end. The groove does not extend up to the very end

Text-figure 5.



Cerberus rhynchops. Dissection of head from the right side. *f.* fang; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. $\times 3$.

of the tooth, it is deep and almost takes the shape of a canal. The mandible contains twenty-two teeth of unequal size.

The Harderian gland is a little peculiar, for the greater part of the outer portion lies under the poison gland. There are three lobes; the external part is cylindrical, tapering at the posterior end, while the other two within the orbit divide into dorsal and ventral portions surrounding the optic nerve.

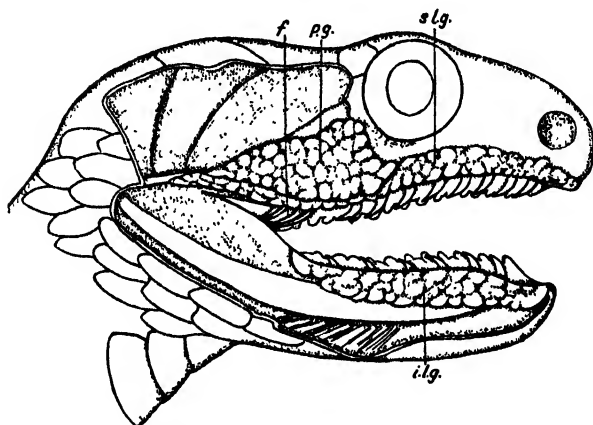
Genus DIPSAS.

DIPSAS TRIGONATA.

The poison gland is clearly distinguishable from the superior labial gland, and anteriorly extends up to about the middle of the eye. The lobules of this gland are smaller than those of the superior labial gland and more distinct. The latter extends to the very end of the mouth anteriorly, and ends posteriorly about the angle of the jaw. It is continuous all along. The inferior labial gland is more highly developed than the superior labial gland, extending far back so that it almost meets the superior labial gland behind the angle of the jaw. The maxilla contains twelve teeth; the last two are grooved. The teeth are larger in front except the first one. The poison fangs are bent considerably backwards and slightly inwards so that the pointed ends are directed towards the pharynx. At the proximal end the grooves of the teeth lie on the outer side, while at the distal end they are in front of it. The grooves extend three-fourths

the length of the tooth. The alternate teeth are hinged and fixed. The mandible contains about thirteen teeth; they are also larger in front, gradually diminishing behind. The

Text-figure 6.



Dipsas trigonata. Dissection of head from the right side. *f.* fang; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. $\times 3$.

Harderian gland consists of three lobes, two within the orbit and the larger part outside.

Genus CHRYSOPELEA.

CHRYSOPELEA ORNATA. (Text-fig. 17.)

The poison gland is very small, smaller than in any opisthophyphous snake I have examined, and it occupies a small area posterior to the eye. The smallness of the gland may be due to the huge growth of the eye. The superior labial gland is well developed, and extends posteriorly further than the angle of the jaw and anteriorly to the very end of the maxilla. The lobules of this gland are larger than those of the poison gland. The inferior labial gland is also fully developed, and is broader at the posterior side. The maxilla contains twenty teeth; the first three are very small, and they increase in size posteriorly; the last two are grooved. The groove is situated on the outer side and is widely open. It arises almost from the base of the tooth, and ends about one-eighth of the length of the tooth from the apex. In section the teeth are nearly oval in shape. The mandible contains twenty-two teeth: the first is very small; there is an increase in size up to the seventh, which is the largest, and then a gradual decrease. Both maxilla and mandible show the alternately fixed and hinged arrangement of teeth.

The Harderian gland consists of three lobes; two portions lie within the orbit and one outside.

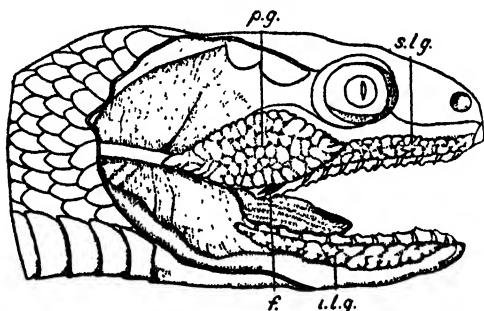
Genus *TARBOPHIS*.

TARBOPHIS VARIEGATUS.

The specimen of this snake was in a damaged condition.

The poison gland is large, and quite distinct from the superior labial gland; it is spindle-shaped, the anterior end lying below the middle of the eye. The superior labial gland is narrow, and reaches the anterior end of the maxilla, where it enlarges and curves round to join the gland of the other side. It is also continuous below the poison gland. The inferior labial gland extends from the very end of the mandible in front, and meets

Text-figure 7.



Tarbophis variegatus. Dissection of head from the right side. *f.* fang; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *s.l.g.* superior labial gland. $\times 3$.

the superior labial gland posteriorly behind the angle of the jaw. Of the nine teeth in the maxilla the last is large and grooved, and the rest are smaller and subequal in size. The grooved tooth is situated far behind within the buccal cavity. The groove is placed on the external surface of the tooth, and does not extend up to the end of the tip. There are about fourteen teeth in the mandible, the series decreasing in size posteriorly. They are alternately hinged and fixed. The Harderian gland consists of two lobes, one outside and the other within the orbit, and it is perforated by the optic nerve.

Genus *PSAMMOPHIS*.

PSAMMOPHIS SIBILANS. (Text-fig. 21.)

The poison gland of this specimen shows the most highly-developed condition among the opisthoglyphous snakes that I have examined; it is a distinct organ, and has assumed a definite shape, being oval. It is comparatively very large. The lobules of the gland are much smaller than those of the superior labial

gland. The latter is continuous below the poison gland, and extends anteriorly to the very end of the snout, meeting its fellow of the other side. Behind it extends further back than the poison gland. The inferior labial gland is also well developed, and has the appearance of a compact body reaching as far as the end of the mandible, and posteriorly it meets the superior labial gland behind the angle of the jaw. The maxilla possesses four medium-sized teeth in front, then two large, solid fang-like teeth, followed by a series of four small equal teeth and finally two large straight fangs. The groove of the posterior maxillary teeth is placed on the anterior face of the tooth, and extends throughout the length of it, ending at the tip. The teeth in the maxilla and the mandible are straight and slightly directed backwards, and they also show an alternating arrangement of hinged and fixed teeth. The Harderian gland consists of two lobes, one outside and the other within the orbit. The latter shows a superficial division into two.

Discussion on the Evolution of the Opisthoglypha.

It is generally admitted that the opisthoglyphous snakes are evolved from the Glauconiidæ, and that the immediate ancestors of the Opisthoglypha are the Colubridæ Aglypha. Boulenger pointed out in the year 1896 (1) "that from Aglyphodont forms, in which the teeth increase in size posteriorly, we are gradually led to the Opisthoglypha, which are only to be distinguished by the presence of more or less deep grooves on the posterior fang-like teeth."

As far as my own observations go, I find that, apart from the gradual increase in the size of the teeth, there is a change concurrently in the structure of the particular tooth which is situated in the posterior portion of the maxilla near the opening of the duct of the parotid gland into the mouth. At the same time, the parotid gland itself undergoes a gradual transformation from a simple structure, distinguishable only from the superior labial gland by its colour, to a separate distinct organ lying detached from it. There also occurs a change in the connection of the duct of the parotid gland with the buccal cavity and the teeth.

My observations are based on a study of the following types, arranged in order:—

<i>Dendrophis pictus.</i>	} Aglypha.
<i>Tropidonotus stolatus.</i>	
<i>Lycodon aulicus.</i>	
<i>Oxybelis fulgida.</i>	} Opisthoglypha
<i>Chrysopelea ornata.</i>	
<i>Dryophis mycterizans.</i>	
<i>Psammodphis sibilans.</i>	

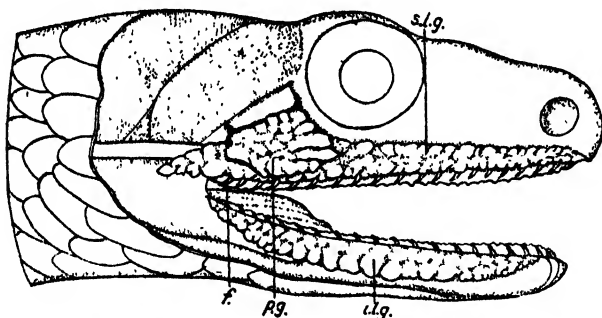
I had hoped to be able to obtain several specimens of both *Xenodon* and *Dispholidus*, in order that a full study might be made of the characters of the "poison apparatus" in these peculiar types. But in this I have been disappointed. I have made some dissections, but it was impossible to obtain a good set of serial sections. So I am unable to determine what further questions might be raised by such a study, or how a complete knowledge of the conditions exhibited by *Xenodon* and *Dispholidus* might affect the general lines of my arguments. However, I hope at some future date to work on these two genera, comparing and contrasting them with the genera I have had the opportunity of studying.

Aglypha.

DENDROPHIS PICTUS.

The anatomy of the general dissection of the glands and teeth of *Dendrophis* is shown in text-fig. 8. Of the two glands in the maxillary region the superior labial gland occupies the greater area, while the so-called parotid gland is confined to a small space. As will be seen, they are so intimately related that it would be difficult to distinguish one from the other but for the colour. This fact struck earlier workers too. Leydig (1873), in his work

Text-figure 8.



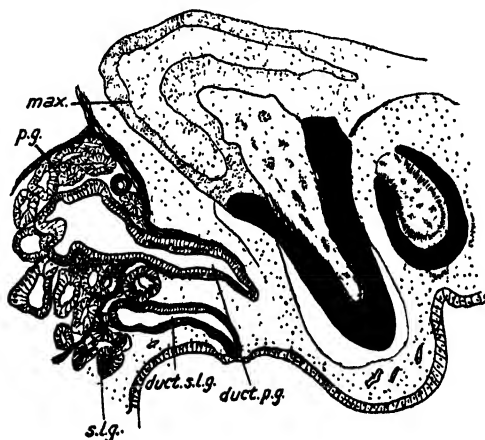
Dendrophis pictus. Dissection of head from the right side. Letters as before. $\times 3$.

on *Tropidonotus*, described that the "superior maxillary gland divides itself into two portions which are distinct in the form and the colour of their follicles; the inferior part is grey and the principal part is of a yellowish colour, and the follicles are larger than on the grey part."

Evidently this yellowish portion becomes specialised to secrete a fluid different from that secreted by the rest of the gland; and we shall see later that this fluid becomes more and more important in the higher snakes as a weapon of defence, and that the teeth become modified to allow of its more careful use.

In the transverse section of *Dendrophis* (text-fig. 9) the superior labial and parotid glands and the ducts arising from them are figured. On comparing these ducts, it will be seen that the duct of the superior labial gland opens into the mouth at some distance from the round peg-like tooth and has no connection with it, while the duct of the parotid gland, formerly forming one of the series of the salivary ducts, has shifted its position in order that it may open nearer to the hinder tooth. In the maxilla there are about twenty teeth, small and almost equal in size; but the

Text-figure 9.



Dendrophis pictus. Transverse section of a portion of the head in the region of the superior labial and parotid glands, showing their ducts. Letters as before. $\times 63$.

hinder tooth, referred to above, is bent backwards at a greater angle than the rest, also a slight cutting-edge has developed on the posterior face.

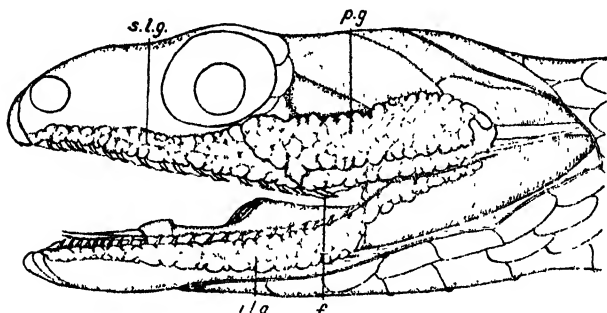
As in all other harmless Batrachians and Reptiles, the teeth are used to prevent the prey from slipping out of the mouth, and at the same time to make small punctures in the body while it is being killed by suffocation. Meanwhile the buccal cavity is flooded with the secretion from all the buccal glands, and the mixed saliva covers the animal and gradually finds its way into the small wounds made by the primitive round teeth.

TROPIDONOTUS STOLATUS.

Text-fig. 10 shows the external features of the gland as seen after the removal of the skin, and also the maxillary teeth from the left side. It reveals a condition strangely advanced in some features, but on the whole distinctly similar to that of *Dendrophis*

(text-fig. 8). Of the more highly-developed parts the parotid gland and the posterior tooth are most striking. The gland (*p.g.*) is quite well developed, and it extends far behind, as far as the angle of the jaw, and in front up to the middle of the eye, while in shape it is peculiar in being rectangular; in fact, as will be

Text-figure 10.

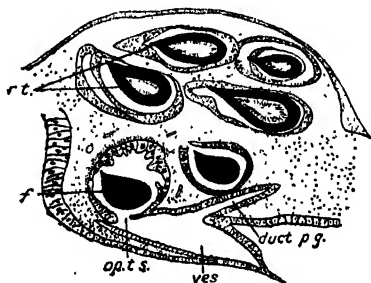


Tropidonotus stolatus. Dissection of head from the left side.

Letters as before. $\times 6$.

seen from the diagram (text-fig. 10), more than half the glandular area in the region of the maxilla has taken up the function of the secretion of the serous fluid. Apart from its great development in size, the dissection shows that the parotid gland is really a part of the superior labial gland, and is only to be distinguished from it by its yellow colour.

Text-figure 11.



Tropidonotus stolatus. Longitudinal section of the head in the region of the poison fang and duct of parotid gland. *f.* fang; *duct p.g.* duct of poison or parotid gland; *op.t.s.* opening of duct into tooth sac; *r.t.* reserve tooth; *ves.* vestibule. $\times 63$.

The maxilla bears about eighteen teeth, these being subequal in size, except the last. This (*f*) is much increased in size, and is more than twice the length of the tooth in front of it. It is

considerably bent backwards. But apart from its being distinguished from the others by its size, it is important to notice that it is separated from them by being enclosed in a special sac (text-fig. 12, *t.s.*) formed from the folding of the mucous membrane; in fact, it has all the external appearance of a fang contained in a tooth sac, and the similarity is so great that it can readily be mistaken for the fang of the poisonous snakes. Further, we can see from the portion of the longitudinal section of the head of *Tropidonotus* that the tooth is specialised by the growth of a cutting-edge on the posterior side. Besides, as in other poisonous snakes, there are reserve teeth (*r.t.*) lying on the inner side of this fang-like tooth. Text-fig. 11 shows the connection of the duct of the parotid gland with tooth and mouth-cavity. It

Text-figures 12 & 13.

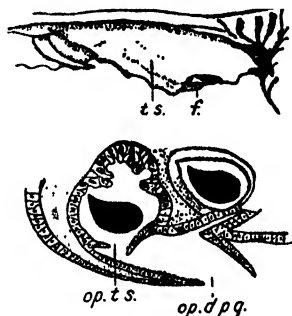


Fig. 12.—*Tropidonotus stolatus*. Tooth sac and fang. *t.s.* tooth sac; *f.* fang.

Fig. 13.—*Tropidonotus stolatus*. Longitudinal section of head in the region of the duct of the parotid gland, showing its opening into the buccal cavity. *op.t.s.* opening of duct into tooth sac; *op.d.p.g.* opening of duct of parotid gland. $\times 63$.

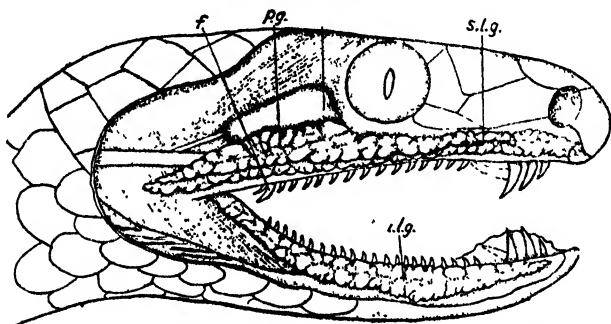
is remarkable that the duct of this gland enlarges at first into a special sac, the vestibule (*ves.*), which is in communication with the tooth sac by an opening (*op.t.s.*). The vestibule opens into the buccal cavity (text-fig. 13, *op.d.p.g.*). Hence we see that the duct, before opening into the buccal cavity, opens into the vestibule, which becomes confluent with the lower part of the tooth sac. By such an arrangement it is made possible for the snake to inject a part of the secretion from the parotid gland into the severe wound at the time when it is being made by means of the sharp cutting-edge of the tooth.

LYCODON AULICUS.

Text-fig. 14 illustrates the general anatomy of the head dissected from the right side. The general survey will show that it is more advanced, and of a higher order than *Tropidonotus* in regard

to its teeth and glands. The parotid gland (*p.g.*) in this snake is much enlarged, and its extension forward goes much further than in *Tropidonotus*, almost to the anterior end of the maxilla. Behind, it extends further than the angle of the jaw, and ends almost on a level with the superior labial gland; in fact, it has taken up so much of the glandular area that the superior labial gland is left reduced to a mere strip of glandular mass, which in dissection has an appearance more or less like that of the poisonous snakes. The lobules of the gland are larger than those of the superior labial gland. This is the only case I have yet met with in aglyphous or opisthoglyphous snakes where the poison gland is so highly developed and extends further forward than the middle of the eye. The most interesting feature to notice is the point of termination of the gland in front; it gradually narrows, and ends with a little bend above the enlarged fang-like tooth, apparently giving an impression in dissection of the duct of

Text-figure 14.



Lycodon aulicus. Dissection of head from the right side. Letters as before. $\times 6$.

proteroglyphous snakes opening at the base of the fang. I hope at some future time, when more material is available, to make a more complete examination of the anterior end of the jaw of *Lycodon*, in order to put to the test Boulenger's suggestion of the probable evolution of the Proteroglypha from the Aglypha.

There are eighteen maxillary teeth, the anterior three are large and are followed by a diastema, the next fourteen are very small, and the last two are large and fang-like, and are enclosed within a muscular tooth sac similar to that already noted in *Tropidonotus*. In the transverse section (text-fig. 15) of the head of *Lycodon* will be seen the section of the posterior tooth sac (*f. & t.s.*). It will be noticed that the tooth is further specialised than that of *Tropidonotus* by the growth of cutting-edges on both sides. These cutting-edges give the appearance of a lancet.

The duct of the poison gland, like that of *Tropidonotus*, opens into the vestibule which communicates with the tooth sac at one end, and at the lower end opens into the buccal cavity (*op. d. p. g.*). A comparison of the course of this duct in *Tropidonotus* and *Lycodon* reveals the fact that in *Lycodon* the communication of the vestibule with the tooth sac is higher than in *Tropidonotus*, so that the secretion of the gland first fills the

Text-figure 15.



Lycodon anlicus. Transverse section of head in the region of the fang, duct of the poison gland and its opening into the tooth sac and the buccal cavity. *ves.* vestibule; other letters as before. $\times 63$.

cavity of the tooth sac while on its course downwards into the buccal cavity. By such an arrangement of the duct the tooth-cavity is kept filled with the poison, and the tooth bathed in it. In this way a greater amount of poisonous fluid can be injected into the bigger wound, which is made by the two cutting-edges of the lancet-shaped tooth.

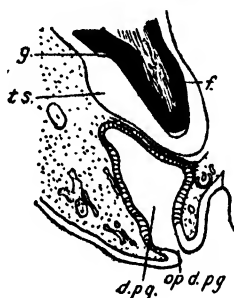
Opisthogylpha.

OXYBELIS FULGIDA.

This is a very interesting snake because of the fact that although it has acquired a better and surer means of injecting poison into the wound by developing a groove in the fang, it still retains the ancestral method of filling the tooth sac with the poison. West has described the anatomy of the head in detail, but for the present purpose of comparison his figures are insufficient. I have been unable to procure any specimens of *Oxybelis* to verify West's observation, and therefore cannot provide the necessary

diagrams. So I have to base my arguments on West's account in the Proceedings of the Zoological Society, 1895. According to West, "the poison gland is very clearly defined and the superior labial gland is exceedingly long and narrow; it reaches to the anterior extremity of the maxilla, and consists of much smaller lobules than the poison gland. . . The maxilla possesses more teeth than that of any other snakes examined, there being twenty in one uninterrupted series. The first seventeen are equal in size and much curved; the posterior three are a little larger, compressed laterally, and the external face of each possesses a very shallow groove. The muscular folds surrounding these three posterior teeth are not united in front, and in consequence of a thin muscular fold across the base of the anterior grooved tooth the poison duct in this snake is placed in communication with the interior of the mouth before it is with the groove of the tooth." (See text-fig. 16.)

Text-figure 16.



Oxybelis fulgida. Transverse section of head in the region of the fang and the duct of the poison gland opening into the mouth (after West). *d.p.g.* duct of poison or parotid gland; *f.* fang; *g.* groove; *op.d.p.g.* opening of the duct of the parotid gland; *t.s.* tooth sac.

West has not given any figure of the dissection of the head, nor any section of the tooth (fang), but from the above description we may surmise from his use of the words "very clearly" that the parotid gland is even more highly differentiated in *Oxybelis* than in *Lycodon*. With regard to the fang, we may safely conclude from the above account of its lateral compression that it still retains some indication of cutting-edges on both sides like those of *Lycodon*, and at the same time has developed in "the external face . . . a very shallow groove." Referring now to the tooth-sac and the duct, I think that the thin muscular fold which West describes is the wall of what I have called the vestibule. Text-fig. 16 shows its connection with the buccal cavity, and probably if another series of sections were examined we should find the openings of the vestibule into the tooth sac. We can infer from

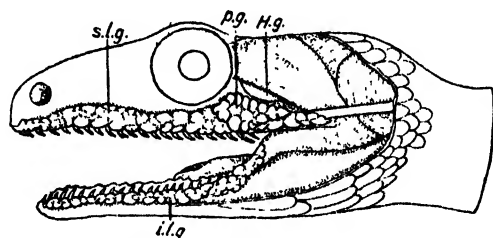
this that the arrangement of the duct, vestibule, and tooth sac is more or less like that of *Lycodon*, and this is emphasized in his figure, which I reproduce.

Oxybelis, therefore, seems to be one of those types which connect the Aglypha with the Opisthoglypha. On the one hand it retains the aglyphous condition of the duct opening into the mouth, and on the other it has the characteristically opisthoglyphous grooved teeth.

CHRYSOPELEA ORNATA.

The general description of the glands and teeth has been given before (p. 304), but for comparison and discussion we will mention some of the facts again. On comparing the external appearance of the poison gland of *Chrysopelea* (text-fig. 17) with that of *Oxybelis*, described by West, and also with that of *Lycodon*, one is struck with the relative reduction in size; in fact, the gland is restricted to a very small area, and in shape and size resembles that of *Dendrophis*, which stands lowest in my series in the Aglypha (p. 307). In other words, it seems to be a case of retrogressive rather than of progressive evolution. But,

Text-figure 17.



Chrysopelea ornata. Dissection of head from the left side. H.g. Harderian gland; i.l.g. inferior labial gland; p.g. parotid gland; s.l.g. superior labial gland. $\times 3$.

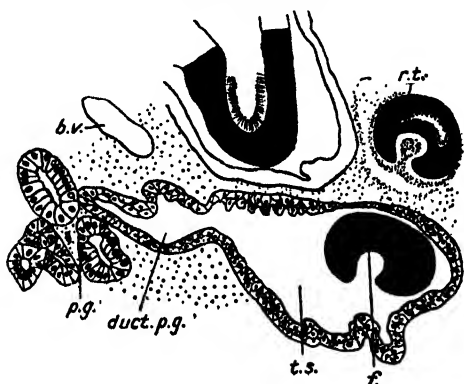
on the other hand, it must be remembered that the snake has acquired more perfection by developing a deeper groove, by means of which it is confident of injecting a sufficient quantity of the poison into the wound, and that therefore it is obviously unnecessary to have a large gland and huge amount of secretion.

It also will be seen that the secretion coming from the gland passes directly into the tooth sac, where greater use can be made of it than if it were squandered in the buccal cavity.

Now, if we examine the transverse section of *Chrysopelea* (text-fig. 18) and compare it with that of *Oxybelis* (text-fig. 16), we find the former specimen is more advanced in many ways. The fang has lost the remains of the cutting-edges on both sides, but has developed a deeper groove than that in the fang of *Oxybelis*.

Regarding the duct, it no longer opens into the vestibule, but directly into the tooth sac. The opening of the vestibule into the mouth cavity is closed, and the tooth sac becomes comparatively bigger. If in text-fig. 16 the opening of the vestibule into the mouth is closed, and at the same time the thin membrane, to which West refers and which is also shown in text-fig. 15, atrophies so that the cavities of the vestibule and tooth sac are confluent with one another, the condition, as shown in text-fig. 18 of *Chrysopelea*, is arrived at. I have shown that the two

Text-figure 18.



Chrysopelea ornata. Transverse section of the head in the region of the poison gland, its ducts, the tooth sac, and the fang. *b.v.* blood-vessel; *duct.p.g.* duct of the poison gland; *f.* fang; *p.g.* poison or parotid gland; *r.t.* reserve tooth; *t.s.* tooth sac. $\times 63$.

cavities really become confluent in *Tropidonotus* and *Lycodon* near to the opening into the mouth. The evidence in favour of the theory that such changes have been brought about is shown by the fact that the duct in *Chrysopelea* opens, not into the mouth, but into the middle of the tooth sac.

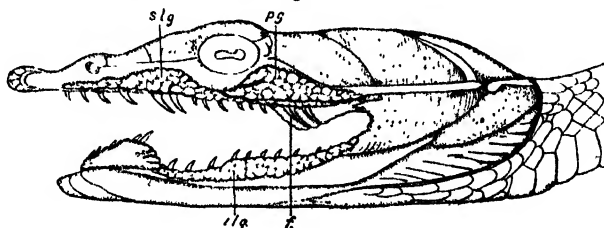
In conclusion, then, we see that *Chrysopelea* is higher in grade than *Oxybelis*, for the reason that the duct of the poison gland opens directly into the tooth sac and that there is a deeper groove in the fang.

DRYOPHIS MYCTERIZANS.

This snake is in many respects much more advanced than *Chrysopelea*. The parotid gland is more highly developed, and has become a distinct organ, though it still remains embedded in the superior labial gland. At the same time, the secretion of the gland becomes more poisonous; it has been proved that the bite of this snake is fatal to small animals (West). The fangs (text-fig. 19) have shifted a little forward in the jaw, and are therefore

in a less concealed position, being rendered capable of inflicting a more severe wound. There are only fourteen teeth in the maxilla: this reduction may possibly be explained by the fact that the teeth, which are present, are large, strong, and more exposed, and better able to kill the prey or to paralyse it quickly with the poison that is now injected directly into the puncture made by the fang.

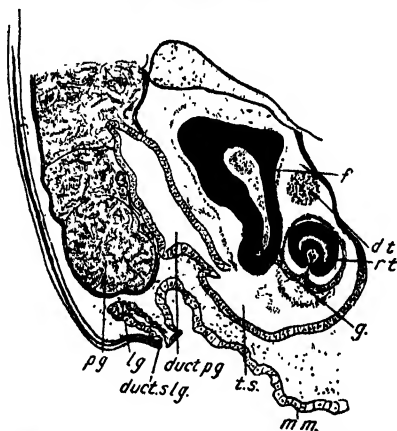
Text-figure 19.



Dryophis mycterizans. Dissection of the head from the left side. $\times 3$.
Letters as before.

In the transverse section (text-fig. 20) we notice that the duct of the poison gland has shifted still further up than in *Chrysopelea* (text-fig. 18), so that its opening into the tooth sac is nearer

Text-figure 20.



Dryophis mycterizans. Transverse section of the head in the region of the parotid and superior labial gland and their ducts, the tooth sac and the fang. *m.m.* mucous membrane; other letters as before. $\times 63$.

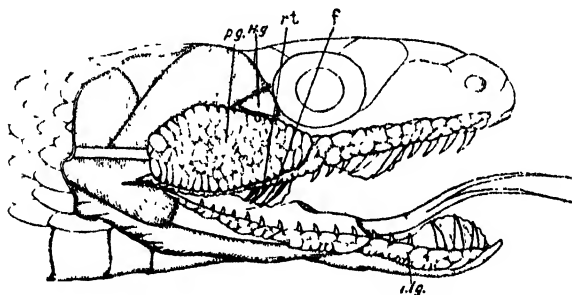
to the base of the tooth and close to the beginning of the groove. The poison coming from the gland passes directly into the groove. In *Dryophis* the groove is now more or less in the shape of a canal, as the edges are almost in contact.

PSAMMOPHIS SIBILANS.

This is one of the most highly-developed of the opisthoglyphous snakes. The very appearance of text-fig. 21 will reveal the fact that it is more ferocious and is capable of doing more harm than *Dryophis*. The structure of the teeth and gland positively prove that it is so, and this is emphasized in the description in the first part of this paper.

Looking at the poison gland, one finds that it has assumed a distinct and definite shape, quite separate from the superior labial gland. The poison fang has moved still further forward in the buccal cavity than in *Dryophis*. It is straighter, and it lies directly below the eye. The shape of the poison fang is of importance, *i. e.* being straight and not bent backward. The fang that is bent backward at an angle is of more use in inflicting

Text-figure 21.



Psammophis sibilans. Dissection of head from the right side. *f.* fang; *H.g.* Harderian gland; *i.l.g.* inferior labial gland; *p.g.* parotid gland; *r.t.* reserve tooth. $\times 3$.

a wound on prey that is already in the mouth, while a straight tooth is of greater use as a weapon of offence and defence, as it can inflict a wound on prey that is outside the mouth. Another improvement has taken place; the groove has become deeper, and extends through the whole length of the tooth, ending at the very tip. It has also shifted from the side of the tooth to the front, in order to be still nearer the opening of the duct, which opens in front of the tooth sac as in the highly-developed poisonous snakes.

It is unfortunate that I have not been able to examine sections of this genus to see the connection of duct with the teeth; but I have seen only one specimen, and it was kindly lent to me by Miss Procter, of the British Museum, for purposes of observation but not for sectioning.

Conclusions.

Taking a general view of this series, it is interesting to endeavour to explain the factors which have brought about the gradual change and complicated modifications leading us to the most highly-developed snakes.

Our hypothetical ancestor of the Aglypha would in all probability be one in which the teeth were equal and peg-like, while the superior labial gland showed no differentiation. The secretion was used more or less for digestive purposes, like the saliva of other animals. The next step in evolution was brought about by the necessity of having a stronger secretion which would have the action of disintegrating the prey more quickly within the mouth. A portion of the gland in the region of the maxilla was differentiated to perform this function. The tooth nearest to the opening of the duct of this gland became a little different from the others by acquiring a cutting-edge, and the duct of this portion moved nearer to it. By this arrangement it became possible for the snake to make a deeper and larger scratch and to pour poison on the wound, as in the case of *Dendrophis*. However, by this method the poison from the now differentiated poison gland is inevitably mixed, and therefore diluted with the general saliva in the mouth. In order to avoid this dilution, the tooth nearest to the opening of the poison gland became bigger and separated from the rest by being enclosed in a special sac. The sac is kept filled with poison, so that the tooth is always immersed in it (*Lycodon* and *Tropidonotus*). This arrangement acted as a sure means of making a deeper wound, which may be compared to poisoning the prey by probing the body with a lancet besmeared with poison. This is undoubtedly a slow process, as a sufficient quantity of poison could not be injected.

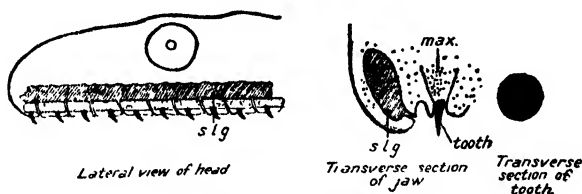
The next step is a great improvement in the tooth—a groove appeared which became almost a canal, as we have seen in *Chrysopelea* and *Dryophis*. At the same time, the gland became a distinct organ (text-fig. 21) from the general glandular mass of the superior labial gland, and the duct moved upward to open finally at the base of the tooth. Evidently this is a great advance, for by this means pure unmixed poison can be injected into the deeper tissue. We may compare this with the modern method of injection by a hypodermic or intermuscular syringe, which acted almost instantaneously. This seems to be the origin of the opisthoglyphous snakes.

But even this method has its defects in some ways. The grooved tooth being situated far behind, the prey has to be taken well into the mouth before the operation can be performed. Besides, this tooth cannot be utilised as an organ of offence and defence. *Dryophis*, in a primitive manner, has overcome this difficulty by developing an extra solid tooth in the anterior end

of the jaw (text-fig. 20) which disables the prey before it is carried further into the mouth to the region of the poison fang. In order to do away with unnecessary apparatus and provide one fang which would serve all purposes, the poison fang has shifted forward right to the front of the mouth, dragging with it the duct of the poison gland. This gave rise to vipers, where we know that the poison apparatus is perfect in all ways and that the other teeth have disappeared. Probably evolution has taken place in this way, as already pointed out by Boulenger: "the series (in Opisthoglypha) culminating in such forms as have the maxillary bone much abbreviated, the solid teeth reduced to two or three, and the fang extremely large and deeply grooved. If we turn to the skull of the least specialised among the Viperidæ, we see that the poison fangs are situated on the posterior extremity of the maxillary bone, close to its articulation with the ectopterygoid, a condition which is identical with that of Opisthoglyphous Colubrids. It is therefore clear to me that the Viperids have been derived from the Opisthoglyphs."

SUMMARY.

Text-figure 22.

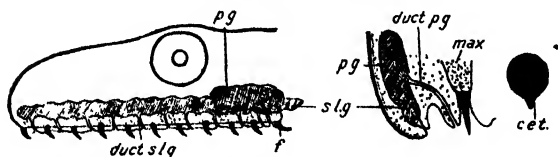


1. Hypothetical ancestor.

Gland in the region of maxilla undifferentiated: teeth all equal and peg-like.

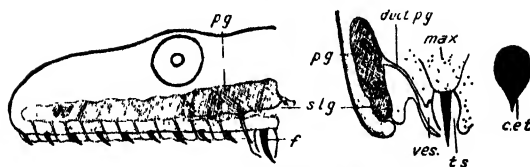
All the ducts open in the buccal cavity far away from teeth.

Text-figure 23.

2. *Dendrophis pictus*.

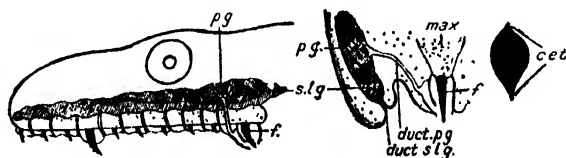
A small portion, near the posterior end, of the gland (*pg.*) differentiated. The duct of this portion moved inward to open near the hinder tooth (*f*). The latter has become different from others by being more bent inwards, and also has developed a slight cutting-edge (*c.e.t.*) on the inner side.

Text-figure 24.

3. *Tropidonotus stolatus*.

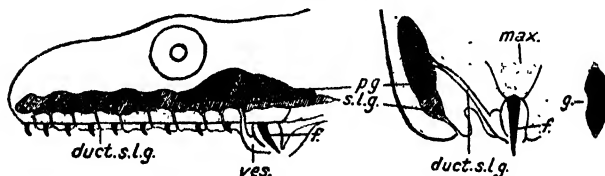
A greater portion of the gland in the region of the maxilla is differentiated to form the parotid or poison gland (*p.g.*). The hinder tooth (*f*) is much bigger than those in front. The cutting-edge (*c.e.*) is more marked. It is also enclosed within a special sac (*t.s.*). The duct of parotid glands (*duct p.g.*) enlarges at the end to form a cavity (*ves.*) which becomes confluent with the tooth sac before opening into the mouth. Sac is kept filled with the secretion and the tooth dipped into it.

Text-figure 25.

4. *Lycodon aulicus*.

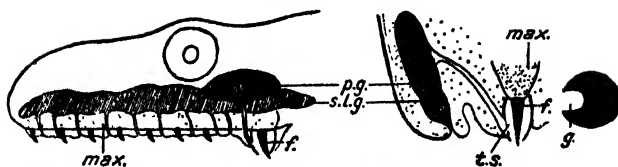
The parotid gland is much enlarged, and almost extends up to $\frac{2}{3}$ of maxilla. The duct (*duct p.g.*) is similar to *Tropidonotus*, except that it opens a little higher. The tooth is like a lancet, with a cutting-edge on each side.

Text-figure 26.

5. *Oxybelis fulgida*.

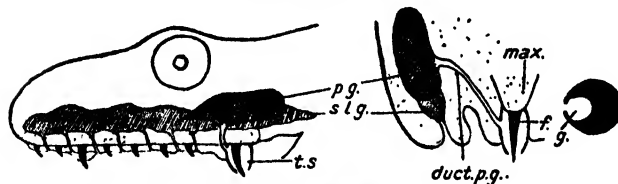
The poison gland (*p.g.*) well developed. The arrangement of the duct is similar to that of *Lycodon* and *Tropidonotus*, i. e. enlarges to form vestibule (*ves.*) before opening into the mouth (Aglyphous condition). The fang (*f*) is laterally compressed. Has almost lost cutting-edges, but has acquired a very shallow groove like Opisthoglypha.

Text-figure 27.

6. *Ohrysopelea ornata*.

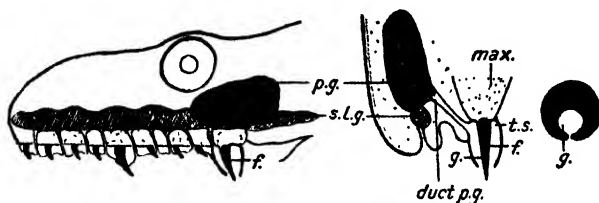
The poison gland is reduced in size, due to the fact that the fang (*f*) has acquired a deeper groove (*g*), through which a greater amount of secretion can be injected into the wound, and there is very little waste. The wall between the vestibule (*ves.*) and the tooth sac has disappeared; at the same time the opening of the duct into the mouth cavity is closed, and hence the duct (*p.g.*) opens directly into the tooth sac.

Text-figure 28.

7. *Dryophis mycterizans*.

The poison gland (*p.g.*) is much more differentiated. The groove (*g*) of the fang is deeper and almost like a canal. The duct (*duct p.g.*) has shifted upward to open into the tooth sac almost near to the base of the fang, which has also moved forward in the mouth cavity.

Text-figure 29.

8. *Psammophis sibilans*.

The poison gland (*p.g.*) is distinct—almost a separate organ. The fang (*f*) is almost straight, and has shifted still further in the mouth cavity. The groove lies in front of the tooth instead of on the side, nearer to the beginning of the groove.

References to the more important Literature.

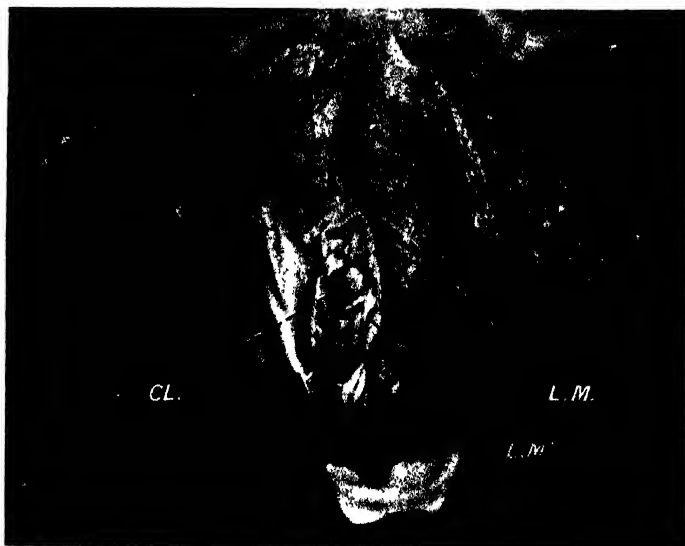
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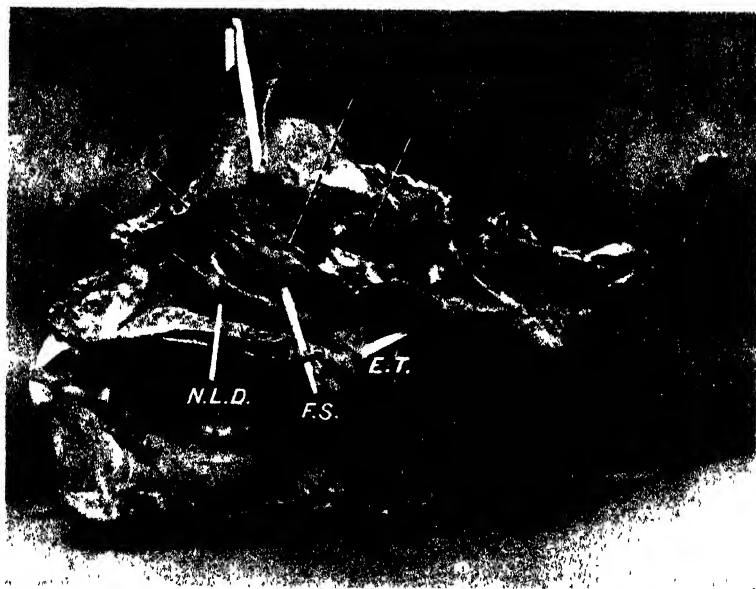
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ANATOMY OF THE CHIMPANZEE.



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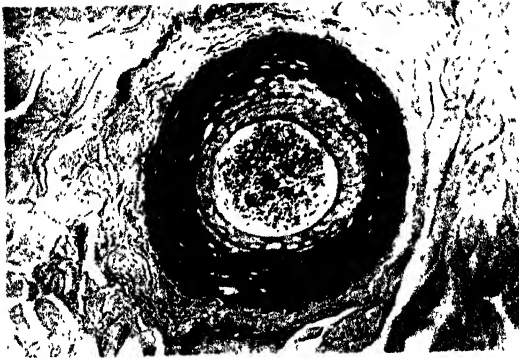


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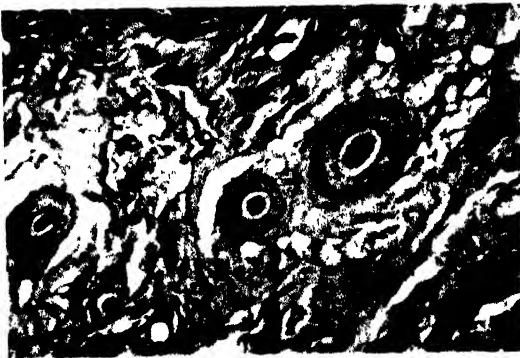
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22. On the Anatomy, Physiology, and Pathology of the Chimpanzee. By CHARLES F. SONNTAG, M.D., F.Z.S. Anatomist to the Society, and Demonstrator of Anatomy University College.

(Plates I.-III.*; Text-figures 25-49.)

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INTRODUCTION.

Zoological literature contains descriptions of parts of nearly three hundred Chimpanzees, but the anatomy of one animal only has been described at any length by Gratiolet (22). His account omits many special points, which have also been neglected by other observers, and the same can be said of the works of Sperino (47) and Vrolik (51), which give accounts of the comparative anatomy of all the Anthropoid Apes. It is, therefore, evident that a full account of one animal is required to serve as a standard for future workers. The present account is based on the examination of a young female, *Anthropopithecus troglodytes*, which died in the Society's Gardens after a residence of two and a half years. And if that species is different from *Troglodytes aubryi* it should be a useful companion to Gratiolet's account of the latter. The animal had the following measurements:—

Length from supra-orbital crests over head and back to anus	23.5 inches
Length from supra-orbital crests toinion	6.4 "
" " inion to anus	17.1 "
Tip of acromion to centre of antecubital fossa .	9.3 "
Centre of antecubital fossa to lower end of radius	9.2 "
Hand (palm 4 ins. : middle digit 3.2 ins.)	7.2 "

* For explanation of the Plates see p. 429.

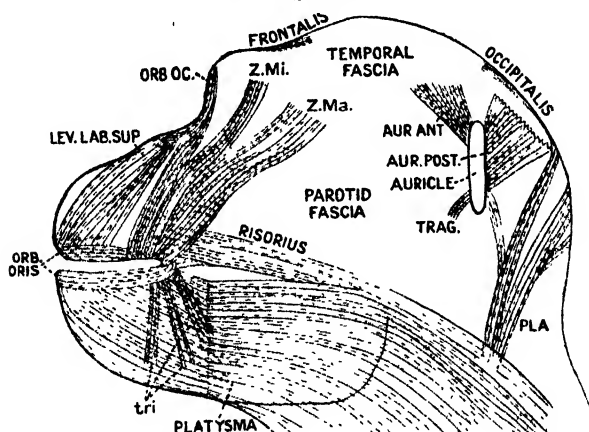
Total length of pectoral extremity	25·7 inches
Great trochanter to centre of patella	9·1 ,,
Centre of patella to lower end of tibia	7·6 ,,
Foot (sole 4·6 ins.: middle digit 2·8 ins.).....	7·4 ,,
Total length of pelvic extremity	24·1 ,,
Excess of pectoral over pelvic extremity	1·6 ,,

THE MUSCULAR SYSTEM.

Muscles of the Head, Neck, and Back.

The *platysma myoides* (text-fig. 25) is much thicker than in Man. It arises from the fascia over the pectoralis major and deltoid, and the two muscles are inseparable in the middle line of the neck. Its lateral parts are more muscular and thicker than the medial portions. About an inch below the symphysis menti the fibres of the mesial parts decussate (Ruge 42, Champneys 11), and I observed the fibres of the left muscle lying superficial to those of the right one; but Quain describes the reverse

Text-figure 25.



Superficial muscles of the face. ORB. OC.: orbicularis oculi; ORB. ORIS: orbicularis oris. Other letters in text.

condition in Man. The fibres are attached to the lower border of the mandible, the skin of the lips, and the muscles of the lips and angles of the mouth. But no fibres are attached to the zygoma as described by Champneys. In the face it separates into upper and lower bundles of fibres; the former, corresponding to the risorius in Man, runs to the muscles at the angle of the mouth; and the latter, which is much larger, blends with the skin and muscles of the lower lip. Small fibres, running from the platysma to the angle of the mouth, correspond to the triangularis muscle (*tri.*).

A fan-shaped muscle separates from the platysma in the neck, runs upwards behind the auricle and spreads out into bundles which are attached to the back of the auricle, the occipital crest, occipitalis muscle, and the deep fascia over the back of the neck. Ruge (42) has given a very elaborate account of the manner in which the platysma enters into the other facial muscles.

Occipito-frontalis (text-fig. 25):—There are many differences of opinion about this muscle. Tyson (50) and Traill (49) could not detect it, Owen (39) found a trace of it, and Wilder (53) found the muscle bellies small, but the aponeurosis was large. Ruge (42) figured a very extensive muscle and a small aponeurosis.

In my specimen the occipitalis arises from the middle two-fourths of the occipital crest, but it is not divisible into two bellies as in Man. The fibres pass forwards for nearly two inches and end in a well-marked aponeurosis. The frontalis arises from the supra-orbital ridges and space between, but is not so well-marked as the occipitalis. It is very easily removed with the skin. It blends with the orbicularis oculi.

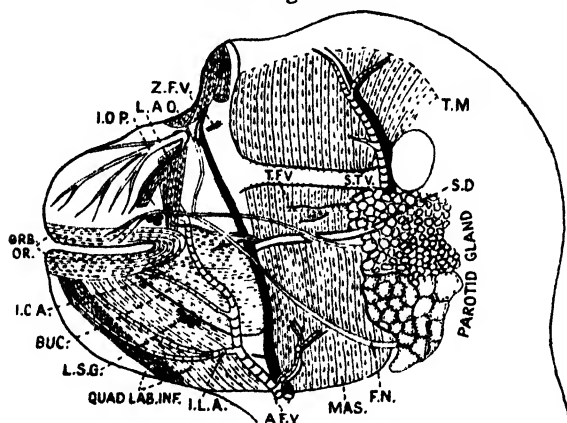
The *Orbicularis oculi* (text-fig. 27 A) is divisible into orbital and palpebral parts as in Man. The former arises from the inner end of the frontal bone and the nasal process of the maxilla; and both muscles are united across the mid line. As it lies on the bones bounding the orbit its upper part is strong and compact and gives off a strong bundle of fibres from its lateral part to enter the zygomatic mass (Z.M.). The fibres on the lower boundary of the orbit are arranged in loose bundles. The palpebral fibres run from the internal tarsal ligament to the lateral tarsal raphé, and are thickened close to the roots of the eyelashes, the thickened parts being of greater dimensions than the ciliary bundles (C.B) in Man. At the lateral tarsal raphé the orbital and palpebral parts are continuous. The nerve-supply from the facial nerve is shown in text-fig. 26.

The lips and cheeks receive many muscles (text-fig. 25), most of which, though thin, are of considerable superficial extent. They are disposed in two layers as in Man, but the characters are very different in a number of points. The superficial layer is composed of the risorius, levator labii superioris, zygomatic mass, orbicularis oris, triangularis and quadratus labii inferioris. The deep layer consists of buccinator, depressor anguli oris, incisivi, canini, mentales, and premolares. The *risorius* is composed entirely of the upper part of the platysma, for no fibres are derived from the fascia over the masseter muscle. It blends with other muscles at the angle of the mouth. The *levator labii superioris* (LEV. LAB. SUP) arises, under cover of the orbital part of the orbicularis oculi, from the entire infra-orbital border of the maxilla. It radiates in a fan-like manner and is inserted into the entire length of the upper lip and upper border of the alæ nasi. The fibres forming the latter insertion correspond to the levator labii superioris alæque nasi of Man. Many of the fibres of the muscle are very thin. Champneys (11) states that it

is not well differentiated from the levator anguli oris, but that is not the case in my specimen; it is only at their insertions that these muscles are fused. Gratiolet (22) describes a mingling of the fibres with those of the orbicularis and they cover the malar-maxillary articulation.

The *zygomatic mass* (text-fig. 25) in my specimen differs from the muscles described by Ruge (42), Gratiolet (22), and Champneys (11). In all the descriptions and published figures it is less powerful, or the parts are more separate. In my specimen it is the most powerful muscle in the face, and has three powerful heads of origin. A strong bundle separates from the orbital part of the orbicularis palpebrarum, the *zygomaticus minor* (Z.Mi)

Text-figure 26.

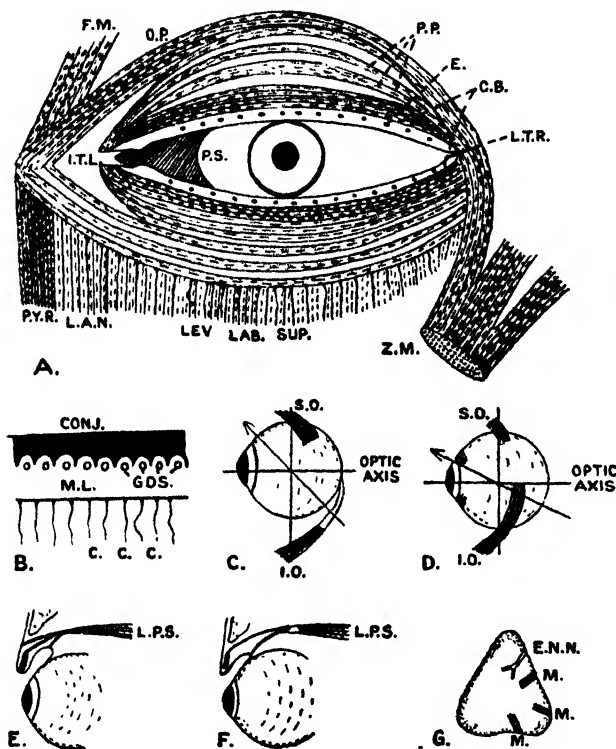


Deep muscles of the face. A.F.V.: anterior facial vessels; F.N.: facial nerve; I.C.A.: inferior coronary artery; L.S.G.: labial salivary glands; M.A.S.: masseter; O.R.B. O.R.: orbicularis oris; S.D.: Stensen's duct; S.T.V. and T.F.V.: superficial temporal and transverse facial vessels; T.M.: temporal muscle; Z.F.V.: zygomatofacial vessels. Other letters in text.

springs from the malar bone and temporal fascia, and the *zygomaticus major* (Z.Ma) arises from the anterior end of the zygoma. The three heads unite to form a strong muscle an inch wide blending with the muscles of the lips and angle of the mouth. It probably does much more work than the proper levator anguli oris. The *quadratus labii inferioris* (text-fig. 26) has a lower origin than in Man. It springs from the posterior half of the lower border of the outer surface of the body of the mandible. It is in contact with the masseter behind and receives fibres from the platysma below. The fibres course upwards and forwards and blend with those of the orbicularis oris. The anterior fibres are fine and close together, and interlace in the front of the lower lip with fibres of the opposite muscle. Running through the

muscle are branches of the inferior labial artery (I.L.A), and the mental branch of the inferior dental nerve emerges from the mandible underneath it. Champneys (11) states that this muscle is not differentiated.

Text-figure 27.



Muscles of the eyelids (A), eyes (C-F) and nose (G); conjunctiva (B). C: cilia; CONJ: conjunctiva; E: eyelids; E.N.N: external nasal nerve; F.M: frontalis; I.O: inferior oblique in the Chimpanzee (C) and Man (D); I.T.L: internal tarsal ligament; L.T.R: lateral tarsal raphé; M.L.GDS: Meibomian glands; O.P: orbitalis; P.S: plica semilunaris; P.P: palpebralis; L.P.S: levator palpebrae superioris of Man (E) and the Chimpanzee (F); S.O: superior oblique muscle.

The *triangularis* (text-fig. 25, *tri.*), although figured as a prominent muscle by Ruge (42), is represented by a few broad fibres passing from the platysma to the angle of the mouth.

The *orbicularis oris* is composed of fibres from all the facial muscles except the levator labii superioris aëque nasi; and it

has the usual sphincteric arrangement. From its deep surface it gives off small muscular slips (text-fig. 27) which are attached to the bones at the bases of the sockets of the incisor, canine and premolar teeth. These are best developed in the upper jaw. Between them and the mucous membrane there are numerous labial salivary glands and branches of the infra-orbital nerve plexus (text-fig. 26, I.O.P).

Between the levator labii superioris and the levator anguli oris numerous branches of the facial nerve and infra-orbital branches of the trigeminal nerve ramify and anastomose, and numerous labial salivary glands are present. The facial nerve supplies the muscles, and the infra-orbital nerves can be traced to both skin and mucous membrane.

The *levator anguli oris* (text-fig. 26, L.A.O) is a small triangular muscle. It arises from the maxilla below the infra-orbital foramen, and is inserted into the orbicularis oris at the angle of the mouth. A small slip passes to the skin of the upper lip. The latter is not mentioned by other authors.

The *buccinator* (text-fig. 26, Buc) arises from the maxilla and mandible close to the roots of the last molar teeth and from the pterygo-maxillary ligament. It emerges from under cover of the ascending ramus of the mandible and blends with the orbicularis oris in both lips; but the fibres do not decussate as in Man. Lying on its surface are a pad of fat, several buccal salivary glands, the buccinator branches of the internal maxillary artery, and the long buccal branch of the trigeminal nerve. It is crossed by the anterior facial vein and external maxillary artery.

Nasal Muscles (text-fig. 27 A):—No nasal cartilages exist*, so the nasal muscles are inserted into the skin. The upper border receives a continuous strip of muscles from the combined orbicularis oculi and frontalis and the levator labii superioris. The former corresponds to the pyramidalis (Pyr) and the latter to the levator labii superioris alaeque nasi (L.A.N). Three small muscular slips arise from each half of the nasal orifice of the skull and are inserted into the deep surface of the skin. No depressor septi nasi is present. The sensory external nasal nerve is seen emerging from the nasal fossa on each side.

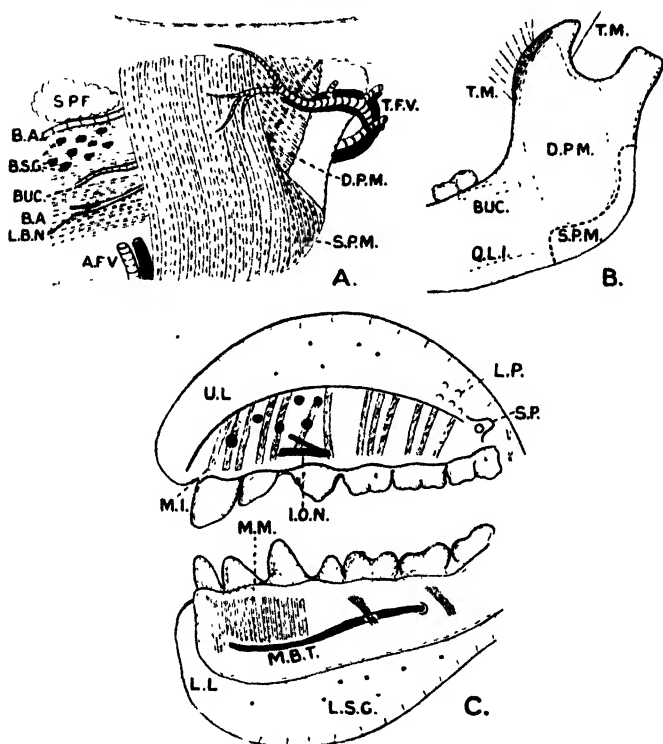
Extrinsic Muscles of the Auricle (text-fig. 25):—Ruge (42) described and figured a superior auricular muscle descending from the vertex of the skull to the root of the pinna, and auriculo-occipital and posterior auricular muscles acting on its posterior part. A small tragus runs to the lower and front part of the pinna. Wilder (53) described an attolens and a combined attrahens and retrahens. In my specimen the attolens (Aur. Ant) arises from the epicranial aponeurosis, and the combined attrahens and retrahens (Aur. Post) arises from the aponeurosis and occipital crest, touching the occipitalis above. The fibres

* This statement is based on both macroscopic and microscopic examination. But future material may show that the conditions here are purely individual in character.

of both muscles are continuous on the root of the pinna. Slips from the platysma (PLA) go to the back of the auricle, and a small tragus (TRAG) is present.

The *masseter* (text-fig. 28 A) consists of the usual superficial and deep parts. The former (S.P.M.) arises from the lower borders of the malar bone and anterior two-thirds of the zygoma :

Text-figure 28.



Muscles of mastication; A : Masseter; B : Attachments of muscles to the mandible; C : Muscles, nerves and vessels below the labial mucous membrane. B.A. and BUC : buccal artery and buccinator muscle; I.O.N., L.B.N., and M.B.T : infra-orbital, long buccal, and mental nerves; L.L. and U.L : lips; M.I. and M.M : incisive and mentalis muscles; L.P. and S.P : labial and salivary papillae; S.P.F : suctorial pad of fat. Other letters as in text-fig. 26.

the fibres pass downwards and backwards to be inserted into the margin of the lower border, angle, and lower half of the posterior border of the ramus of the mandible. Between the two parts is a strong fascial sheet into which fibres of both parts are inserted. The deep part (D.P.M) arises from the entire length of the deep

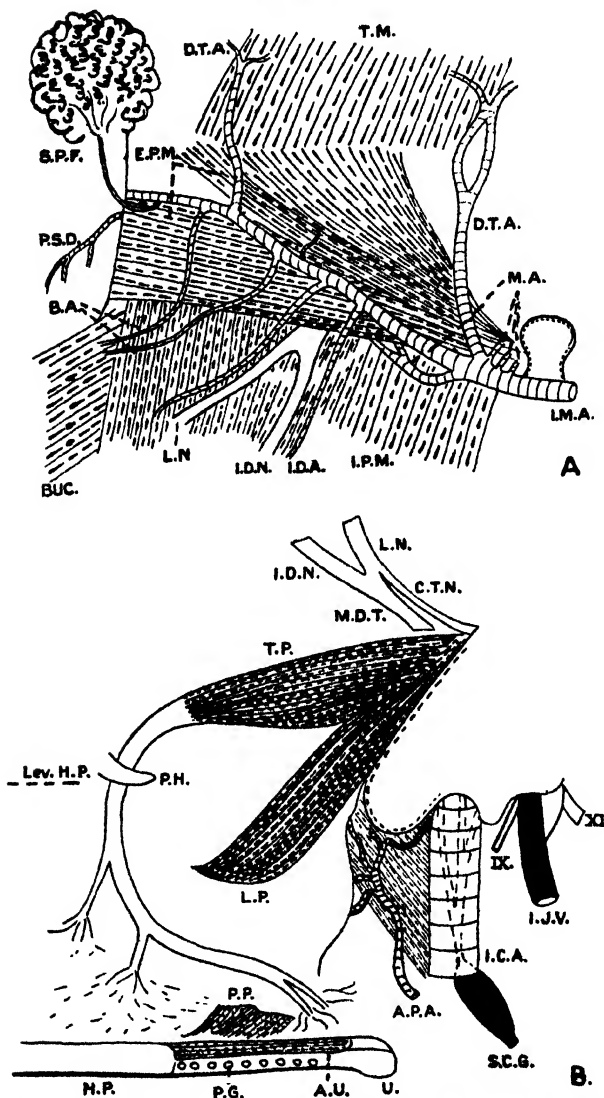
surface of the zygoma, and the fibres converge to be attached to the anterior two-thirds of the outer surface of the mandibular ramus and coronoid process. Numerous large vessels (T.F.V) ramify between the masseter and parotid gland and supply both. The actual insertions are shown in text-fig. 28 B.

The *temporal muscle* is large and powerful. It arises from the entire temporal fossa from the external angular process of the frontal bone in front, to about four centimetres behind the concha and upwards to a point level with the supra-orbital crest. It also arises from the temporal fascia which covers it. The fibres are strong, coarse and mixed with tendinous bands; they converge to be inserted into the anterior border, point and posterior border of the coronoid process (text-fig. 28 B). The anterior part of the muscle is attached by muscle fibres to the anterior border of the process, which is of considerable length. But the posterior part is attached by aponeurosis to the backwardly-directed point and short posterior border. On the surface of the muscle the zygomatico-facial artery ramifies. A piece of the aponeurotic insertion sweeps over the outer surface of the coronoid. The deep temporal vessels anastomose within it. The action of the temporal muscle is described at length by Gratiolet. The attachments of the masseter and temporal muscles to the mandibular ramus are shown in text-fig. 28 B. The *temporal fascia* is attached to the temporal crest, external angular process of the frontal bone, malar bone and upper border of the zygoma. It is overlain by a considerable deposit of fat. It gives an attachment to the fibres of the zygomaticus minor and extrinsic muscles of the auricle. A few fibres of the temporal muscle arise from it.

The *pterygoid muscles* (text-fig. 29 A) are very similar to those in Man, and all authors who have described them come to similar conclusions. The relations of the various nerves in the pterygoid region are the same as in Man, and the internal maxillary artery (I.M.A) crosses the outer surface of the external pterygoid (E.P.M) as in some human bodies. The veins, however, do not form a large diffuse plexus, but consist of tributaries accompanying the large arteries and opening into an internal maxillary vein. It divides into two veins which unite with the superficial temporal vein. It communicates with the anterior facial vein and with deep veins in the neck. No lymphatic glands are present in the pterygoid region, but much fat is present. It is, therefore, evident that, with the exception of the characters of the veins, the pterygoid region is essentially similar to that in Man.

The *sterno-mastoid* (text-fig. 30, S-M.M) arises by a long, gently tapering, strong tendon from the inferior border of the manubrium sterni, and it does not develop muscular fibres till it reaches the neck. A few small tendinous bundles run from the tendon of origin to the upper and mesial aspects of the sterno-clavicular articulation, and strong fascia unites the tendon to the

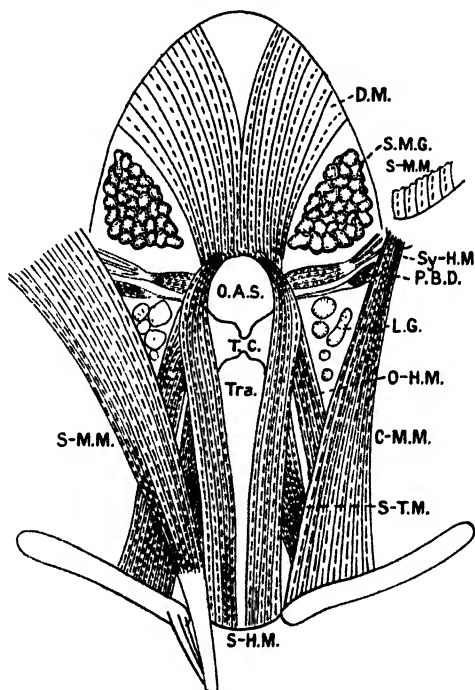
Text-figure 29.



Pterygoid (A) and Palatal (B) regions. E.P.M. and I.P.M.: external and internal pterygoid muscles; A.P.A.: ascending pharyngeal artery; I.M.A.: internal maxillary artery (letters of branches on p. 384); I.C.A.: internal carotid artery; I.D.N.: inferior dental nerve; I.J.V.: internal jugular vein; C.T.N.: chorda tympani joining the mandibular nerve (M.D.T.); H.P.: hard palate dropped for diagrammatic purposes below its true level (lev. H.P.); P.G.: palatal glands; P.H.: pterygoid hamulus; S.C.G.: superior cervical sympathetic ganglion; IX, XI: cranial nerves.

inner end of the clavicle. It gives attachment to a few fibres of the pectoralis major, but it is not enveloped by the latter as described by Gratiolet and Alix (22). In the neck it forms a wide, comparatively thin muscle, whose fibres are coarse. It is inserted into the outer half of the superior curved line of the occipital bone, overlapping the trapezius. No fibres are attached to the mastoid process. Between the sterno-mastoid and subjacent cleido-mastoid there are muscular branches of the

Text-figure 30.



Muscles of the middle of the neck. L.G: lymphatic glands; O.A.S: opening into the air-sac from the ventricles of the larynx; O-H.M: omo-hyoid muscle; S.M.G: submaxillary gland; S-T.M: sterno-thyroid muscle; T.C: thyroid cartilage; Sy-H.M: stylo-hyoid muscle; Tra: trachea. Other letters in text.

occipital artery. The external jugular vein does not cross the surface of the muscle, and the transverse cervical nerve, after emerging from beneath the cleido-mastoid, runs forwards over the surface of the sterno-mastoid. The sterno- and cleido-mastoids are separate throughout, though closely apposed and surrounded by fascia.

The *cleido-mastoid* (text-fig. 30, C-M.M) arises from the inner third of the upper border of the clavicle. As it passes upwards

in the neck it becomes narrower and is inserted into the outer surface of the mastoid process. The muscle raises a prominent ridge on the anterior wall of the air-sac. Many vessels and nerves pierce the deep fascia at the lateral border of the cleido-mastoid; and the spinal accessory nerve passes into its deep surface in the upper third.

When an incision is made through the platysma and deep fascia the wall of the air-sac makes its appearance. The wall varies in thickness in different parts, and its lining is smooth and moist. It consists of a central part with two lateral diverticula. The central part extends upwards to the hyoid bone, and downwards to the lower border of the manubrium sterni between the tendons of origin of the sterno-mastoid muscles. Its anterior wall is covered by the platysma, and the larynx, trachea and pre-tracheal muscles shine through the thin posterior wall. The lateral parts are very capacious, and have large circular orifices under cover of the cleido-mastoids. When these are explored the finger can pass along the greater part of the deep surface of the pectoral muscles and the inner border of the deltoid; it palpates the entire length of the clavicle, the head of the humerus, the glenoid cavity, and borders of the scapula. Many muscles, nerves, and the carotid sheath form ridges in the walls of the sac.

The *omo-hyoid* (text-fig. 32 A) is more complex than in Man, and it is more complex in my specimen than in others described. It consists of three bellies. The postero-mesial belly is tapering. It arises from the back of the first costal cartilage along with the sterno-thyroid muscle, with which it is considerably fused. The anterior belly is tapering, and inserted into the lower border of the hyoid bone at the side of sterno-hyoid. The postero-lateral belly, which is the strongest, arises from the upper border of the scapula close to the root of the coracoid process. All three bellies meet in a Y-shaped junction, and a tendinous thread runs into sterno-hyoid.

The *sterno-hyoid* (text-fig. 30, S-H.M) arises from the back of the upper part of the manubrium sterni, and is inserted into the lower border of the hyoid bone. The opposite muscles first diverge and then converge, and fibres pass between them on the hyoid bone. The *sterno-thyroid* arises from the back of the manubrium sterni and first costal cartilage and is inserted into the upper part of the thyroid ala. Some fibres pass into the thyro-hyoid muscle.

The *digastric muscle* (text-fig. 30, D.M) is transitional between Parson's first and third types. The anterior bellies are only separate in front. They are fused behind where they arise from the front of the body of the hyoid bone. Each belly is inserted into the anterior two inches of each half of the mandible. The posterior belly is bulky, but the tendon (text-fig. 30, P.B.D), which enters the postero-lateral part of the anterior belly immediately in front of the hyoid bone is long and slender. It arises from

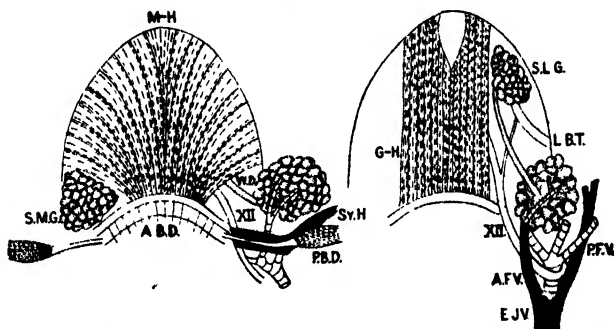
the depression on the temporal bone corresponding to the digastric fossa in Man. Chaîne (10) has recently described the digastric muscle. The tendon of the posterior belly tunnels the stylo-hyoid muscle; it has no direct attachment to the hyoid bone as described by Gratiolet (22).

Some fibres of omo-hyoid and sterno-hyoid pass into the anterior bellies of the digastrics.

The *stylo-hyoid* arises by one large and several small tendons from the styloid process and bone around. It is long, thin, fleshy, and wrapped round the digastric tendon. It is inserted into the upper border of the hyoid bone opposite sterno-hyoid and omo-hyoid.

The *mylo-hyoid* (text-fig. 31, M-H) arises from the upper border of the hyoid bone under cover of, but never fused with,

Text-figure 31.



Anatomy of the submental region (No. 1). A.B.D: anterior belly of the digastric turned down; A.F.V: anterior facial vein; E.J.V: external jugular vein; L.B.T: lingual nerve; P.B.D: posterior belly of the digastric; P.F.V: posterior facial vein; S.M.G: submaxillary gland; Sy.H: stylo-hyoid muscle; W.D: Wharton's duct. Other letters in text.

the anterior belly of the digastric. The level of origin corresponds to the extent of the insertions of the sterno-hyoid and omo-hyoid on the posterior border. The fibres radiate to be inserted into the inner surface of the mandible. The posterior fibres lie just in front of the submaxillary gland. Lying on the surface of the muscle and supplying it are branches of the submaxillary twigs of the external maxillary artery. I did not observe any decussation of fibres in the middle line as described by Gratiolet (22).

No submental lymphatic glands were found behind the symphysis menti.

The *genio-hyoid muscles* (text-fig. 31, G-H) are separated anteriorly close to their origins from the lower part of the genial fossa on the back of the symphysis menti. In the greater part of

the interramal space the two muscles are in contact in the mid line. They are inserted into the upper border of the body and part of the great cornu of the hyoid bone. At their sides lie deposits of fat surrounding the sublingual glands (S.L.G.), the numerous arteries to these glands, and the large lingual branch of the trigeminal nerve (L.B.T.). The latter is seen vanishing under cover of the genio-hyoid muscle. The hypoglossal nerve (XII) also is seen dividing into branches which pass under the muscles and sublingual glands. When the genio-hyoidei are reflected it is seen that a well-marked bursa, capable of lodging the tip of the index finger, lies between them and the hyoid bone anteriorly and the genio-glossi posteriorly; and there is a thick fatty septum between the two genio-glossi. The hyoglossi crossed antero-posteriorly by the strong, thick, stylo-glossi; the sublingual glands and the hypoglossal and lingual nerves are further displayed. The former is seen giving two branches to its corresponding genio-hyoid.

The *genio-glossi* (text-fig. 32, G.G) are two long, narrow, thick muscles arising from the bottom of the genial fossa. They are separated in the mid line by a comparatively thick deposit of fat, and a considerable interval separates each from the mandible. In that space the entire sublingual gland, the hyoglossus and styloglossus muscles, the lingual and hypoglossal nerves and the lingual artery are seen. The artery emerges from under the hyo-glossus. Some fibres of the genio-glossi reach the hyoid bone under the hyo-glossus.

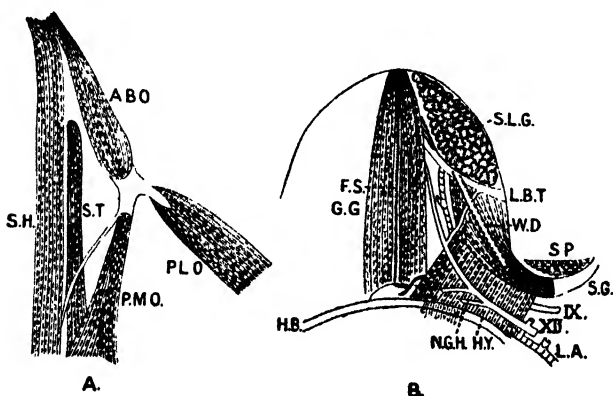
The *hyo-glossus* (text-fig. 32, HY) arises from the lateral part of the body and the whole of the great cornu of the hyoid bone, but the origin from the body does not spread over a half as stated by Gratiolet (22). The fibres pass upwards to be inserted into the side of the posterior half of the tongue under the stylo-glossus. It is not fused with the opposite muscle, but fibres of the thyro-hyoid can be traced into it. A great part is concealed by the stylo-glossus. The relations are very similar to those in Man.

The *stylo-glossus* (text-fig. 32, S.G) is relatively more powerful than that in Man. It arises by a short, rounded strong tendon from the outer surface of the base of the styloid process. It describes a curve as in Man, and its volume increases greatly as it is traced forwards. It gains an attachment to the side of the tongue from the level of the outer border of the hyo-glossus behind to nearly the apex of the tongue in front. It covers the upper half of the hyo-glossus, and it extends from the side of the tongue above to the outer border of the genio-glossus below. The part anterior to hyo-glossus is concealed by the large sublingual gland, with the lingual branch of the trigeminal nerve curving round its posterior pole. The connecting loop between the lingual and hypo-glossal nerves crosses it anteriorly, and Wharton's duct (W.D) crosses it obliquely from above downwards and behind forwards.

The *superior constrictor of the pharynx* is continuous above and

in front with the buccinator, both being attached to the pterygo-mandibular ligament. It is attached to the mylo-hyoid line on the mandible, the internal pterygoid plate, the base of the tongue, the mucous membrane of the floor of the mouth and the bucco-pharyngeal aponeurosis. The lower border is overlapped by the middle constrictor, and the stylo-pharyngeus passes between them as a few separate, but thick, bundles of fibres. Some of these fibres pass into, and blend with, the outer surface of the superior constrictor. The upper part of the muscle is separated by a large sinus of Morgagni from the base of the skull, but the levator palati and tensor palati, which are situated therein, lie horizontally, whereas they are more vertical in Man, and of smaller size. The constrictor is attached above and behind into

Text-figure 32.



The omo-hyoid muscle (A) and the anatomy of the submental region (B). A.B.O., P.L.O., and P.M.O.: anterior, postero-lateral and postero-mesial bellies of the omo-hyoid muscle; F.S.: fatty septum; L.A.: lingual artery; N.G.H.: nerves to the genio-hyoid muscle; H.B.: hyoid bone; S.H. and S.T.: sterno-hyoid and sterno-thyroid muscles; IX and XII: cranial nerves. Other letters as in text-fig. 31.

the basis cranii. It is difficult, and in some places impossible, to separate the superior constrictor from the stylo-glossus muscle which courses downwards and forwards on its outer surface.

A well-marked bundle of fibres passes towards the angle of the mouth. The *middle constrictor of the pharynx* arises from the deep surface of the hyoid bone in the angle between the greater and lesser cornua, and it is inserted into the mid-dorsal line of the pharynx, its fibres mingling with those of the opposite muscle. It is overlapped by the inferior constrictor. Some fibres of the stylo-pharyngeus pass into its outer surface. Between the superior and middle constrictors there is a non-muscular area anteriorly. The *inferior constrictor of the pharynx* arises as in

Man from the oblique line on the thyroid cartilage and from the side of the cricoid. Its fibres sweep more or less upwards, overlap the lower border of the middle constrictor and blend with the opposite muscle in the mid-dorsal line. It has no origin from the first tracheal ring as in Gratiolet's specimen (22).

The *stylo-pharyngeus* (text-fig. 32, S.P) arises from the tendon of the stylo-glossus, but Gratiolet (22) states that it rises from the base of the styloid apophysis. It splits up into bundles some of which are inserted into the superior and middle constrictors, others passing between these muscles and radiating in the wall of the pharynx. The glosso-pharyngeal nerve hooks round it and sends it a well-marked branch.

The *levator palati* and *tensor palati* (text-fig. 29 B) arise by a strong, common musculo-aponeurotic origin from the apex of the petrous temporal bone, the under surface of the Eustachian tube and the scaphoid fossa. So the separate origins of the muscles have fused in this animal. The *levator palati* (L.P) runs downwards and forwards and spreads out between the layers of the palato-pharyngeus. The *tensor palati* (T.P) is even more horizontal. Its tendon winds round the pterygoid hamulus and is inserted by several small tendinous and fascial bundles in the palatal aponeurosis. The complete limits of the *palato-pharyngeus* (P.P) could not be accurately made out, and the *palato-glossus* hardly exists. The *azygos uvulae* (A.U) ends posteriorly in membrane as pointed out by Gratiolet (22).

The *thyro-hyoid* runs from the entire width of the thyroid ala to the under and outer surfaces of the body and great cornu of the hyoid bone. Its nerve from the hypoglossal is well marked.

The *scalenus anticus* arises from the anterior tubercles of the transverse processes of the third, fourth, and fifth cervical vertebrae, but others have given its origin from 4, 5, and 6. It is connected by a tendon to the rectus capitis anticus major. It is inserted as in Man, the tubercle on the first rib being lateral to the chondro-costal junction. The *scalenus medius* and *scalenus posticus* arise as in Man. They unite to form a flat sheet which courses downwards to be attached to the outer surfaces of the first five ribs. The fusion and extent are greater than that described by Gratiolet (22) and others. It is crossed posteriorly by the slips of insertion of the upward continuation of the sacro-spinalia.

The *omo-trachelian* runs as usual from the transverse process of the atlas to the upper and outer aspect of the acromion. It has been recorded by some as being not an omo-trachelian, but as an acromio-basilaris.

Muscles and Fasciae of the Back.

The fascia covering the trapezius and latissimus dorsi is of great strength, especially below. It is attached above to the occipital crest, mesially to the vertebral spines and below to the

iliac crest. It is continuous with the fascia over the gluteal muscles. Laterally it is continuous with deep fascia of the neck, thorax and limbs.

The *trapezius* arises from the inner third of the occipital crest, the external occipital protuberance, all cervical spines, the thirteen dorsal spines and the supraspinous ligament. There is no ligamentum nuchæ, so the origin differs from that in Man. Various authors have recorded it as arising from the first ten or twelve dorsal spines. The lower border is not fused with the *latissimus dorsi*, as described by Champneys (11), Bland Sutton (4), and others, though some anatomists did observe fusion. Close to the lower angle of the scapula there is a triangle of auscultation similar to that in Man. The whole origin is muscular, there being no aponeurosis close to the vertebral spines as there is in Man. It is inserted into the outer third of the posterior border of the clavicle, some fibres passing into the deltoid, the outer border of the acromion and the whole length of the spine of the scapula. The most lateral part of the spinous insertion is aponeurotic. There is no differentiation of fibres inserted into a special area on the root of the spine of the scapula as there is in Man. The spinal accessory nerve can be traced almost to the lower border of the muscle, and gives off numerous branches to it. It communicates with the third and fourth cervical nerves, but there is no marked sub-trapezial nerve plexus. It divides at the root of the neck into two marked branches. One of these goes to the cervical part of the trapezius and the other to the thoracic part.

The *latissimus dorsi* arises from the lower five dorsal spines and supraspinous ligaments, the posterior lamella of the lumbo-dorsal fascia and the posterior lip of the iliac crest from the highest point to the anterior superior spine, where it overlaps the outer border of the external oblique. It also receives slips from the ninth, tenth and eleventh ribs, but none from the inferior angle of the scapula. On the ribs, whence it derives slips, it fuses with the origin of the external oblique. The strong tendon is inserted into the floor of the bicipital groove on the humerus, and is extensively fused with the *teres major* and *dorso-epitrochlearis*. No band runs across the axillary vessels. Bland-Sutton (4) emphasises the absence of the latter slip. Champneys (11) gives the costal origin as ribs 10-13, and mentions a lesser adhesion to the *teres major*. Hepburn (24) gives its origin from the anterior half of the outer lip of the iliac crest, and records three costal slips; he also mentions slight fusion with the *teres major*.

The *rhomboideus* is an undivided sheet arising from the last two cervical and first four dorsal spines. It is inserted into the lower three-fourths of the vertebral border of the scapula. The insertion reaches higher than the root of the spine of the scapula, and its upper part overlaps the insertion of the *levator anguli scapulæ*. Gratiolet (22) described the origin as extending from

the occiput to the seventh dorsal spine. The sheet is undivided into major and minor muscles, in which it agrees with that described by Gratiolet (22), Vrolik (51), Macalister (33), Bland-Sutton (4), and Wilder (53). Champneys (22) describes major and minor rhomboids in great detail.

The *levator anguli scapulae* (text-fig. 33, L.A.S) arises by five slips from the posterior tubercles of the first five cervical vertebrae, the first being the largest. The lower three origins are tendinous and fused with splenius cervicis. It is inserted into the upper fourth of the vertebral border of the scapula. It is not adherent to serratus magnus, nor is it divisible into two parts. Champneys (11) gives the origin as the first two cervical vertebrae; Gratiolet (22) gives it as the second and third; Hepburn (24) records origins from three cervical vertebrae; Wilder (53) gives it as in Man, and Bland-Sutton (4) records it as springing from the first five.

The *serratus posticus superior* (text-fig. 33, S.P.S) arises by a thin aponeurosis from the spinous processes of the seventh cervical and first dorsal vertebrae, and it is inserted by four muscular slips into the outer surfaces of the first four ribs at their angles. Macalister (33) describes it crossing the first two ribs to be attached to the third and fourth. The *serratus posticus inferior* arises from the posterior lamella of the lumbo-dorsal fascia and sweeps antero-laterally to be inserted into the lower borders of ribs nine to thirteen just external to their angles. Bland-Sutton (4) gives its attachments as ribs nine to twelve.

The *lumbo-dorsal fascia* is arranged as in Man. The thoracic part is thin and transparent, and it is difficult to separate it off from the subjacent muscles as a continuous sheet. The lumbar part is very dense and strong. The posterior lamella is not easily separated from the latissimus dorsi, to which it gives origin. Posterior branches of the spinal nerves pass through its deep surface. In its lower part it gives origin to the serratus posticus inferior. Between the outer and middle lamellae the erector spinae is present, and the attachments of the middle lamella are as in Man. The quadratus lumborum lies between the moderately strong middle lamella and the weaker internal lamella, whose attachments to the arcuate ligaments of the diaphragm are as in Man.

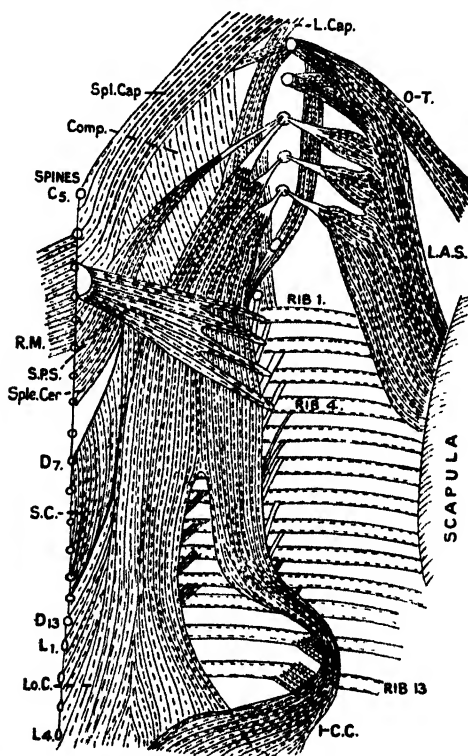
In the possession of a serratus posticus inferior the Chimpanzee resembles Man, and that muscle is one of the three characteristically human muscles. It will be seen later that the Chimpanzee possesses the plantaris, which is the second human muscle, but it does not possess the peroneus tertius.

The muscles of the back described above are relatively stronger than in Man, and they are relatively weaker than the pectorales, but the total bulk of these groups has probably diminished during captivity.

The *splenius* (text-fig. 33) arises from the sides of the tips of the fifth, sixth, and seventh cervical vertebrae, and from the spines

of the first seven dorsal vertebræ. All the origin is muscular except that from the sixth and seventh cervical vertebræ. The greater part becomes splenius capitis (Spl.Cap.) which is inserted into the mastoid and outer part of the superior curved line of the occipital bone, and a small slip runs into the first head of the levator scapulæ. The splenius cervicis (Sple.Cer.) consists of one digitation which joins the third head of the levator scapulæ.

Text-figure 33.



Muscles of the back. Comp : complexus; R.M : rhomboides.
Other letters in text.

Other observers give the splenius cervicis insertions into the first four cervical vertebræ.

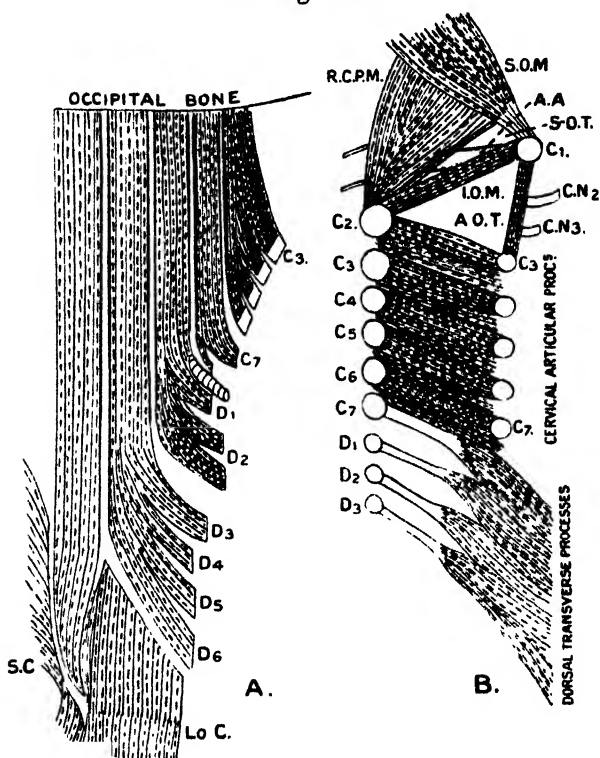
The *sacro-spinalis* (erector spinæ) is divisible into three columns—an outer ilio-costalis, a middle longissimus, and an internal spinalis—but their characters differ from those of the corresponding muscles in Man. The outer and middle columns are intimately fused at the origin of the muscle; they separate in the lumbar and greater part of the thoracic region; in the upper

thoracic and lower cervical regions they are fused; and the combined mass eventually breaks up again into muscular slips. The inner column separates off in the upper thoracic region. The *ilio-costalis* (text-fig. 33, I-C.U) arises with the subjacent *longissimus* from the iliac crest between the highest point and the posterior superior spine, and it derives fibres from the covering posterior lamella of the lumbo-dorsal fascia. It gives two slips to the lower borders of the twelfth and thirteenth ribs, of which the former is the larger. It receives a large number of muscular slips from the outer surfaces of all the ribs, the size of the latter diminishing from below upwards. Many of the small muscular slips are continuous with the slips given off from the *longissimus*. From the outer border of the muscle long, slender tendons run to the lower borders of the angles of the first nine ribs. The *longissimus* (text-fig. 33, Lo.C) arises from the crest of the ilium from the highest point to the posterior superior spine, the posterior sacro-iliac ligament, the back of the sacrum, all sacral and lumbar vertebral spines and the spines of the twelfth and thirteenth dorsal vertebræ. It gives slips to the lower borders of ribs 4 to 13 between their angles and the transverse processes. The attachments to the first three ribs come from the combined *longissimus* and *ilio-costalis*. The combined outer and middle columns divide into slips which are attached to the posterior tubercles of the transverse processes of the third, fourth, and fifth cervical vertebræ along with the levator angulæ scapulæ. The third cervical vertebra thus receives *splenius cervicis*, levator anguli scapulæ and *longissimus*. The part of *longissimus* attached to these processes corresponds to *longissimus cervicis* in Man, but is not so extensive. The *spinalis dorsi* (text-fig. 33, S.C) is a narrow muscle arising from the *longissimus dorsi* and the eleventh and twelfth dorsal spines. It is inserted by muscular and tendinous fibres into the first eight dorsal spines. Between it and the *longissimus* is a triangular space into which the complexus passes and fuses with both. The *longissimus capitis* (text-fig. 33, L.Cap) is relatively stronger than in Man. It arises from the first six dorsal transverse processes by tendinous and muscular slips. It is fused with the *longissimus dorsi*, complexus and *scalenus posticus*. It breaks up into slips which are inserted into the posterior tubercle of the atlas and the occipital bone below the crest. On the atlas its insertion is fused with the levator scapulæ and omo-trachelian.

The *complexus* (text-fig. 34 A), lying under the *longissimus capitis*, has a very extensive origin from the articular processes of the lower five cervical vertebræ, the upper six dorsal transverse processes and the *longissimus* and *spinalis dorsi*. It forms a number of closely-set parallel muscle bundles which are inserted into the inner half of the occipital bone below the superior curved line. It is not separable into a biventer cervicis and complexus as in Man. No slip springs from the seventh cervical spine.

The *semispinalis* (text-fig. 34 B) has an origin from the articular processes of the lower five cervical vertebræ by broad bands, and from the transverse processes of all dorsal vertebræ, the lower five origins being tendinous. It is inserted into the spinous processes of cervical vertebræ two to six by muscle fibres (*semispinalis colli*) and to the seventh cervical and first three dorsal spines by tendons (*semispinalis dorsi*). It is practically

Text-figure 34.



Muscles of the back. A: complexus; B: semispinalis and suboccipital muscles.

A.A: posterior arch of atlas; C.N₂ and C.N₃: posterior divisions of the second and third cervical nerves; Lo.C: longus colli; S.C: spinalis; S.O.T: suboccipital triangle. Other letters in text.

impossible to distinguish accurately the limits between these muscles in the combined origins.

A well-marked muscular slip runs from the third articular process to the transverse process of the atlas and forms a triangle with the inferior oblique and semispinalis (text-fig. 34, A.O.T). It alters the course of the second and third cervical nerves. The mass of the transverse process of the atlas separates it from the

origin of the *rectus capitis lateralis*, and the latter is the only muscle whose fibres run in the same direction*.

The *multifidus spinæ* extends from the sacrum to the axis. It arises from the sacrum, sacro-iliac ligament, mammillary processes of the lumbar vertebræ, transverse processes of all dorsal vertebræ, and lower four cervical articular processes. It is inserted into the spines of all vertebræ except the atlas. The *semispinalis* covers it but its fibres, which run in the same direction, are longer than those of the *multifidus*, and extend to vertebræ farther apart. The cervical fibres of the *multifidus* do not form broad bands.

The *obliquus inferior* (I.O.M) and *obliquus superior* (S.O.M) (text-fig. 34 B) are as in Man.

The *rectus capitis posterior major* (text-fig. 34, R.C.P.M) is a powerful pyramidal muscle quite concealing the minor muscle. It arises from the spinous process of the axis and is inserted into the occiput below the entire length of the superior oblique. The *rectus capitis posterior minor* arises from the inner three-quarters of an inch of the posterior arch of the atlas and is inserted into the occipital bone below the major muscle. It is quite concealed by the latter, and by the approximation of the walls of the sub-occipital triangle. *Rectus capitis lateralis* is as in Man.

Interspinales, intertransversarii and levatores costarum are as in Man. Rotatores dorsi are twelve pairs of fan-shaped muscles running from the transverse processes of the dorsal vertebræ to the laminae of the vertebræ above them, the first one being inserted into the seventh cervical lamina.

Muscles of the Thoracic Parietes.

The *external intercostal muscles* run in the same direction as those in Man. They extend from the angles of the ribs to the sternum in the first three and last two spaces. But there are external intercostal membranes in the other spaces. The *internal intercostals* do not differ materially from those in Man. The *triangularis sterni* arises as in Man from the back of the ensiform cartilage, and it is inserted by radiating slips into the sternal ends of the second, third, fourth, fifth, and sixth ribs. It has a slightly different relation to the internal mammary artery from that in Man, the details being given with that vessel on page 386.

The *sternalis* muscle is absent. Some authors describe it, and their observations have been collected by Keith (29).

Contrary to the conditions in Man, there is a well-marked lateral branch of the first intercostal nerve. It runs over the pectoralis major and fades away among the glands in the axilla.

Prevertebral Muscles.

The *longus colli* consists, as in Man, of vertical, superior, oblique and inferior oblique portions. The vertical part arises from the

* This is probably an individual peculiarity.

lower two cervical and upper four dorsal vertebræ, and is inserted into the bodies of the second, third, and fourth cervical vertebræ. The lower oblique portion runs from the first four thoracic to the fifth and sixth cervical vertebræ. And the upper oblique part runs from the third, fourth, and fifth cervical vertebræ to the anterior arch of the atlas. The *rectus capitis anticus major* runs from the third, fourth, fifth, and sixth cervical vertebræ to the basi-occiput. It receives a well-marked slip from the scalenus anticus. The *rectus capitis anticus minor* and *rectus capitis lateralis* are as in Man.

It is, therefore, evident that the facial muscles, the muscles of the back, the scaleni, and the prevertebral muscles are relatively stronger and more intimately united than in Man. This must necessarily make the muscular movements less numerous and not so fine as in him. The muscles forming the suboccipital triangle are crushed together.

Muscles of the Pectoral Extremity.

The *pectoralis major*, which is less powerful than in Man, consists of clavicular, costo-sternal, and abdominal parts. The clavicular part consists of superficial and deep portions. The former arises from the inner half of the front of the clavicle and the outer side of the tendon of the sterno-mastoid; the latter springs from the inner part of the lower surface of the clavicle and fuses with the former, and with the deep surface of the costo-sternal part. The costo-sternal portion arises from the whole length of the body of the sternum and the first six costal cartilages; it fuses with both the external oblique and the abdominal part of the *pectoralis major* at the lower borders of the fifth and sixth costal cartilages. The abdominal part fuses with the external oblique as far as the *linea semilunaris*; it also gets origins from the lower borders of the fifth, sixth, and seventh costal cartilages. The abdominal portion joins the deep surface of the sternal portion to form a muscle which joins the deep surface of the clavicular part. The combined muscle has a musculo-aponeurotic insertion into the inner border of the pectoral crest, the lower part of the capsule of the shoulder joint and the deep fascia of the arm. It is never fused with the deltoid.

I agree with Champneys (11) and Macalister (33) that there is no actual separation between the clavicular and costo-sternal parts such as occurs in Man. Champneys records a special slip arising from the fourth and fifth cartilages, but that is not the case in my specimen.

The delto-pectoral triangle contains the external anterior thoracic nerve, thoracic axis vessels, and tendon of the *pectoralis minor*. It has no lymphatic glands nor the cephalic vein, which are present in Man. Bland-Sutton (4) states that the groove between the *pectoralis major* and deltoid is absent.

The *pectoralis minor* appears to vary considerably both in origin and insertion. In my specimen it arises by three well-marked slips from the lower borders of the second, third, and fourth costal cartilages. Its long, but strong, tendon passes through a fibrous and synovial sheath over the coracoid process, and it is inserted into the upper and back part of the capsule of the shoulder joint. The sheath is adherent to the inner and upper parts of the coracoid process. Champneys (11) gives its origin from the first four ribs and its insertion into the capsule of the shoulder joint close to the supra-spinatus tendon, and Humphry (26) mentions it as extending across to the great tuberosity of the humerus. Bland-Sutton (4) describes an insertion similar to that in my specimen, but gives its origin as ribs three, four, and five. Wilder (53) and Gratiolet (22) record tendons inserted into both the coracoid process and capsule of the shoulder joint, and the latter gives the origin as ribs two to five inclusive. So if several animals are examined the muscle appears to write its evolutionary history.

The *serratus magnus* arises by eleven digitations from the first eleven ribs, the first one being very small, but it has a remarkably rich supply of nerves (text-fig. 48). The first nine arise from the outer surfaces of the ribs, but the tenth and eleventh arise from the lower borders. The digitations arising from the fifth to the eleventh ribs interdigitate with the external oblique. The muscle is thick at its insertion into the deep aspect of the vertebral border of the scapula. The part arising from the first four ribs is much thinner than the remaining part of the muscle. Champneys (11) has given the origin as from the first ten ribs, and described the muscle as consisting of three parts, which he describes in great detail, but Wilder (53) describes two parts, and gives the origin from all the ribs.

The *subclavius* arises from the upper border of the first costal cartilage immediately internal to the rib. It is inserted into the under surface of the second quarter of the clavicle from the inner end. It is enveloped as in Man by the costo-coracoid membrane.

The *costo-coracoid membrane* is attached to the first costal cartilage round the tendon of origin of the subclavius, to the inferior surface of the sterno-clavicular joint, to the under surface of the clavicle by two layers which enclose subclavius as in Man, and to the anterior surface of the clavicle lateral to the subclavius. The costo-coracoid ligament is well marked. Several authors have recorded the latter. The clavi-pectoral fascia extending downwards from the costo-coracoid ligament splits to enclose the pectoralis minor, and at the same time it sends a process inwards to the neuro-muscular bundle in the axilla. External to the pectoralis minor the fascia passes to the deep fascia of the axilla, and it passes mesially to the deep fascia covering the serratus magnus between the pectoralis major and latissimus dorsi. The membrane is pierced by the external

anterior thoracic nerve and the thoracico-acromial vessels, but it is not pierced by the cephalic vein which runs through it in Man and many other mammals. The fibres run transversely below the costo-coracoid ligament.

The *deltoid*, covered by dense fascia, is coarsely fasciculate. It arises from the front of the outer half of the clavicle and the outer border of the acromion process. A second part has an extensive aponeurotic and fascial origin from the whole length of the lower border of the spine of the scapula, and from the fascia over the entire infra-spinatus. At the inferior angle of the scapula the fascial origin blends with serratus magnus, the rhomboids, teres major, and latissimus dorsi. It conceals a bursa which intervenes between the acromion and upper end of the humerus, but does not communicate with the shoulder joint. One large and several small branches of the circumflex nerve, and branches of the circumflex arteries are seen entering its deep aspect. Humphry found it adherent to the brachialis anticus (26), but Macalister (33) denied that it adheres to the triceps and brachialis anticus. Wilder (53) points out that the attachment to the fascia over the infra-spinatus and the axillary border of the scapula enables the animal to swing the arm far back. The muscle fibres all converge to be inserted into the usual deltoid area on the shaft of the humerus. The insertion is embraced by the brachialis anticus.

Scapular Muscles:—All observers are agreed that the infra-spinatus greatly exceeds the supra-spinatus in size, and both arise from the whole of the scapular fossæ to which they are attached. They are inserted as in Man into impressions on the great tuberosity. Corresponding vessels and nerves pass into them as in Man. The infra-spinous fossa is deep, being enclosed between the prominent spine and a thickening of the axillary border of the scapula. The *teres minor* arises from the lower border of the lip of the glenoid cavity and lateral half of the axillary border of the scapula. It is inserted into the lowest part of the great tuberosity of the humerus and the upper half inch of the shaft of the bone. Champneys (11) gives its origin as the mid third of the axillary border and the adjacent part of the infra-spinous fossa, and Hepburn (24) records its origin from the upper two-thirds of the axillary border. The *teres major* arises from the medial half of the axillary border of the scapula, and is inserted into the inner lip of the bicipital groove. It is strongly fused with the latissimus dorsi. The *subscapularis* arises from the whole of the subscapular fossa, and tendinous bands run through between the bundles of fibres to the bone. It has no origin from fascia over it. The muscular mass converges, and is inserted by three tendons into the lesser tuberosity and the shaft of the humerus over a quarter of an inch below it. Some of the deep fibres are directly inserted into the capsule of the shoulder joint.

The *coraco-brachialis* is fleshy throughout. It arises along with the short head of the biceps from the tip of the coracoid

process, and it is inserted into an impression over an inch long on the inner aspect of the shaft of the humerus. In its upper part it is separated by a cellular interval into two parts, and the musculo-cutaneous nerve passes through the gap. No coraco-brachialis brevis was present. Some fibres go to the internal intermuscular septum and dorso-epitrochlearis, and Hepburn (24) suggests that these represent the coraco-brachialis longus. The part running to the inner surface of the shaft of the humerus corresponds to the coraco-brachialis medius. No coraco-brachialis brevis was recorded by Champneys (11), Bland-Sutton (4), Dwight (18), and Wilder (53), but it was seen by Macalister (33) and Hepburn (24). Bland-Sutton gives its insertion into the upper third of the shaft of the humerus and the capsular ligament. Wilder states that it arises from the coracoid process through the medium of the short head of biceps.

The *biceps* arises as in Man, but the bellies remain separate till they reach the junction of the lower and middle thirds of the arm. In the upper part of the forearm there is a slight bicipital fascia (lacertus fibrosus). The muscle fibres of the combined bellies end in a stout, ribbon-like tendon which is inserted into the posterior part of the radial tuberosity.

The *brachialis anticus* is connected by a strong fascial band to the pectoralis major near its insertion. The origin is as in Man and embraces the insertion of the deltoid. A slip is given to the fascia of the forearm. The fibres converge to an insertion into the coronoid process and inner border of the olecranon.

The *dorso-epitrochlearis* is a thin muscle, a little more than half an inch wide, springing from the junction of the muscular and tendinous parts of the latissimus dorsi. Fibres pass into its upper part from the coraco-brachialis. It passes into the inner side of the internal intermuscular septum in the lower third of the arm, and the latter connects it to the internal condyle.

The *triceps* differs considerably from that in Man. The long head arises from the dorsal aspect of the outer quarter of the axillary border of the scapula. The outer head arises from the upper extremity of the shaft of the humerus and lower part of the capsule of the shoulder joint. The inner head arises from the proximal third of the shaft of the humerus along a linear strip. After a course of two inches the long and outer heads fuse to form a fleshy belly, and this receives the inner head an inch more distal. The muscle is inserted by muscular and tendinous fibres into the tip and dorsal surface of the olecranon, a bursa intervening between the muscle and the capsule of the elbow joint.

A broad bundle of fibres arising from the deep surface of the distal half-inch of the triceps runs to the capsule of the elbow joint and represents the *subanconeus*.

Champneys (11) states that the triceps, anconeus, and sub-anconeus are as in Man. Hepburn (24) mentions that the triceps is as in Man except for the outer head, and mentions that the anconeus is present.

The *palmaris longus* is absent in both arms in this specimen. Traill (49) only noted it in one of the arms in his example. Many authors describe it as being similar to that in Man.

The *pronator radii teres* has both humeral and coronoid heads of origin, and the median nerve dips between them. The head from the internal condyle of the humerus is fused with the origin of the flexor carpi radialis, and the coronoid head is fused with the deep aspect of the flexor sublimis digitorum. It is inserted into the middle third of the outer border of the shaft of the radius, and a few fibres at the upper extremity are inserted into the inner aspect of the supinator brevis. The upper part of the insertion is tendinous, but the remainder is muscular. Throughout its whole length it is fused with fibres of the flexor carpi radialis. No fibres arose from the dorso-epitrochlearis, but a few spring from the extreme distal end of the internal intermuscular septum. Macalister (33) alone states that there is no coronoid head of origin.

The *flexor carpi radialis* has an extremely long origin by a thick muscular belly, which is intimately fused with the pronator radii teres and flexor sublimis digitorum. In the second fourth of the forearm it has no bony attachment, but many fibres run downwards from the pronator teres and flexor sublimis to its tendon. Below that it is attached by muscle fibres to the radius on the inner aspect of the insertion of the pronator teres, and fibres pass downwards from it to the flexor sublimis. The tendon receives muscle fibres on its deep aspect till it reaches the annular ligament. It passes through a tube in the ligament and is inserted into the palmar aspect of the bases of the second and third metacarpal bones. It has a well-marked synovial sheath fused with the anterior annular ligament.

The *flexor carpi ulnaris* arises by a narrow head from the internal condyle, by an expanded head from both internal condyle and olecranon, and by fascia from the upper fourth of the shaft of the ulna. It is inserted into the pisiform bone. It is relatively larger than in Man, and the pisiform is very large.

The *flexor sublimis digitorum* appears to differ considerably. In my specimen it has a very extensive origin from the humerus, ulna, and radius; and fibres spring from those of the other flexor muscles. The humeral head, arising from the internal condyle of the humerus, fuses with the flexor carpi radialis, and receives a few fibres from the flexor carpi ulnaris. It is prolonged almost entirely into the tendons for the ring and little fingers, the tendon for these digits separating off in the middle of the forearm. The coronoid head is fusiform and quickly ends in a tendon which forms the slip to the index finger. The second finger gets its tendon from a muscle which arises from the lower two-thirds of the shaft of the radius and from the flexor carpi radialis. Hepburn (24) states that the tendons to the third and fourth digits come from the radial part of the muscle, while those for the second and fifth come from the ulnar part; and the tendon

for the index goes under those for the second and fourth digits. Champneys (11) states that the middle finger alone has a separate radial origin, but Rolleston gives the radial origin to the tendon for the index. Macalister (33) observed no radial origin at all. Moore (36) states that the annularis receives two tendons, and the minimus gets none. Finally, Bland-Sutton (4) describes the flexor sublimis tendons going to the third, fourth, and fifth digits, but there is a flexor sublimis indicis arising from both radius and coronoid. Dwight (18) describes a very complex muscle. The tendons split over the heads of the metacarpal bones, surround the deep flexor tendons, and are inserted as in Man into the middle phalanges.

Muscles of the Hypothenar Eminence (text-fig. 35 A & C):—The *abductor minimi digiti* (A.M.D) arises by a broad, but thin, muscular origin from the pisiform bone. It lies along the ulnar border of the hand and is inserted by a long, slender tendon into the ulnar aspect of the base of the first phalanx of the little finger. Its insertion is closely blended with that of the flexor brevis. The *flexor brevis minimi digiti* (F.B.M.D) has a single head of origin from the anterior annular ligament and hook of the unciform; and the annular ligament appears to be prolonged into it. It is inserted along with the abductor. The *opponens minimi digiti* (O.M.D) has a double origin from the anterior annular ligament and uncinat process of the unciform, the latter being blended with the flexor brevis. It is inserted into the ulnar aspect of the shaft of the fifth metacarpal bone. The *palmaris brevis* is very extensive in both hands, but several authors describe it as in Man.

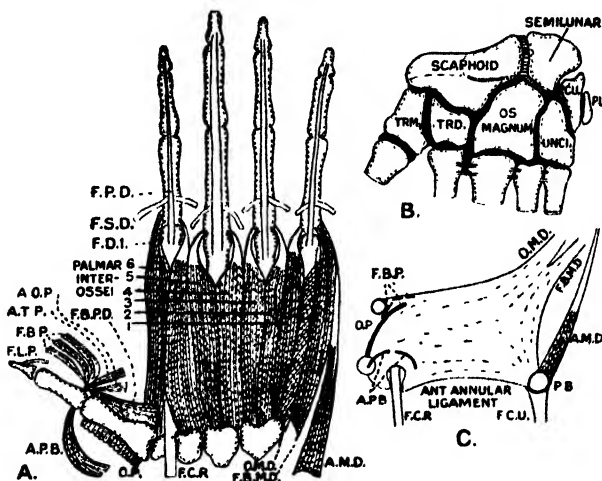
Muscles of the Thenar Eminence (text-fig. 35 A & C):—The *abductor pollicis brevis* (A.P.B) arises from the anterior annular ligament, the scaphoid and sesamoid bone and the sesamoid bone of the thumb, and it is divided into two slips. These unite to a muscular insertion into the radial side of the base of the first phalanx of the thumb. It conceals the lateral half of the opponens. Champneys (11) and Macalister (33) saw no splitting into Scemmering's slips. The *opponens pollicis* (O.P) arises from the anterior annular ligament and ridge of the trapezium. It is inserted into the distal half of the radial aspect of the shaft of the metacarpal of the thumb. Embleton (19) states that the opponens pollicis is absent. The *flexor brevis pollicis* (F.B.P) consists of superficial and deep parts. The superficial part arises by three slips from the anterior annular ligament and trapezium. The deep part arises from the ulnar side of the first metacarpal and anterior annular ligament. Both parts unite and are inserted into the ulnar side of the base of the first phalanx. The whole muscle forms a large mass between the opponens superficially and the adductores deeply. The *adductor transversus pollicis* (A.T.P) and *adductor obliquus pollicis* (A.O.P) are as in Man.

The *flexor longus pollicis* (F.L.P) arises from the inner surface of the shaft of the radius over the whole length except the

proximal inch, and from the interosseous membrane. Some fibres fuse with the flexor sublimis. It has a strong tendon to the palmar aspect of the terminal phalanx of the index, and a very fine tendon to the corresponding part of the pollex. This agrees with the descriptions of Champneys (11), Hepburn (24), and others.

The *flexor profundus digitorum* arises from the inner side of the olecranon, the inner surface of the upper two-thirds of the shaft of the ulna and the interosseous membrane; and some of the fibres fuse with the flexor sublimis and flexor carpi ulnaris. The strong tendon divides into three tendons running to the palmar aspects of the terminal phalanges of the third, fourth,

Text-figure 35.



The muscles and joints of the hand. F.B.P.D.: deep part of the flexor brevis pollicis; F.C.R.: flexor carpi radialis; F.C.U.: flexor carpi ulnaris; F.D.I.: first dorsal interosseous muscle; F.P.D.: flexor profundus digitorum; F.S.D.: flexor sublimis digitorum. Other letters in text.

and fifth digits. There is no continuity with the flexor longus pollicis. Several authors have described similar conditions.

The *pronator quadratus* runs downwards and outwards from the lower inch and a half of the front of the shaft of the ulna to the lower inch of the front of the shaft of the radius. Fibres wrap round both bones and extend down to the interosseous membrane.

Lumbricales:—These arise as in Man, and the general disposition is similar, but a well-marked muscular slip connects the first and second. The first and second muscles have long origins from the flexor tendons, but the second and third muscles quickly

separate from the tendons. The insertions are as in Man. Hepburn (24) and Macalister (33) describe them as in Man. Wilder (53), Dwight (18), and Champneys (11) state that the tendon for the minimus arises from the profundus tendon to the annularis.

The *supinator longus* arises from the external supracondylar ridge and from the shaft of the humerus as high up as the insertion of the deltoid. Some fibres come from the external muscular septum, and some from the brachialis anticus. It has a long tendon which is inserted into the shaft of the radius half an inch above the styloid process. Some authors have recorded slightly less or a little more extensive origin and insertion. This animal agrees in this respect with Hepburn's account (24).

The *extensor carpi radialis longior* arises from the lower part of the external supracondylar ridge and septum. Its tendon separates very high up in the forearm, passes under the extensors of the thumb, and is inserted into the radial side of the dorsal aspect of the index metacarpal, and along the radial aspect of the proximal half inch of the bone. This insertion is more extensive than in some accounts.

The *extensor carpi radialis brevior* arises from the lateral epicondyle, the external lateral ligament of the elbow joint and the fascia over the extensor communis digitorum. It is slightly fused with the long extensor. It is inserted into the dorsal aspect of the base of the third metacarpal by three small tendons.

The *extensor communis digitorum* arises from the external epicondyle, the fascia over it, and the intermuscular septa on either side. It remains fleshy to the posterior annular ligament. The origin from the internal septum is particularly strong. It is quite separate from the subjacent extensors. It separates into three broad tendons to the index, medius, and annularis, and a slender tendon goes to the minimus. Close to the heads of the metacarpals there is strong lateral fusion between the tendons to annularis and minimus. The tendons are inserted into the bases of the ungual phalanges. Wilder (53), Vrolik (51), Moore (36), and Macalister (33) deny the presence of a tendon to the minimus. Dwight (18) and Champneys (11) say there is a slip between the tendons to annularis and minimus. The tendons have very powerful thickened expansions into the sides of the interphalangeal joints.

The *extensor minimi digiti* has a long, slender muscular belly enclosed in a strong fascial tunnel. It arises from the fascia over the anconeus, and from the common extensor origin from the external epicondyle. A common dorsal expansion unites its tendon to the innermost communis tendon over the head of the fifth metacarpal. The expansion is very firmly adherent to the capsule of the metacarpo-phalangeal joint. The insertion is into the base of the ungual phalanx of the minimus.

The *extensor carpi ulnaris* is as in Man. Several authors describe this.

The *extensor indicis* arises from the inner surface of the lower fifth of the radius, and some fibres blend with the *extensor longus pollicis*. Its long, and very slender tendon blends with the dorsal expansion of the communis tendon to the index over the first phalanx. No slip goes to any other digit, as in Wilder's specimen (53). Hepburn (24), Macalister (33), and Humphry (26) found it supplying the medius too.

The *supinator brevis* is wrapped round a little more than the upper third of the radius. It is musculo-tendinous.

The *extensor ossis metacarpi pollicis* and *extensor primi internodii pollicis* have a common origin from the bones of the forearm. The latter arises from the upper third of the lateral border of the ulna, and the former from the upper two-thirds of the mesial border of the radius. The tendons separate from the combined muscular mass. The broad tendon of the former runs to the trapezium and thumb sesamoid, and the slender tendon of the latter goes to the base of the metacarpal of the thumb.

The *extensor secundi internodii pollicis* (*extensor pollicis longus*) arises from the third fourth of the inner surface of the shaft of the ulna below the *extensor primi internodii pollicis* and above the *extensor indicis*. Its long, ribbon-like tendon is inserted into the base of the unguis phalanx of the thumb. Hepburn (24) gives its insertion as the base of the first phalanx, but Humphry (26), Macalister (33), Vrolik (51), Wilder (53), and Wyman (54) recorded conditions as in my specimen.

Interossei:—All authors agree that the dorsal interossei are as in Man, and several have described the six interossei on the palmar surface of the manus. Hepburn (24) has shown that three of the six muscles are the true palmar interossei, namely, those to the ulnar side of the index and the radial sides of the annularis and minimus. The others to the sides of the medius and ulnar side of the annularis are abductors, belonging really to the dorsal series. With his observations I am quite in agreement. The six palmar muscles form a very thick stratum. The conditions are shown diagrammatically in text-fig. 35 A. The first dorsal interosseous wraps round the metacarpal of the index. Taking the deep muscles from within outwards, we find:—

1. Opponens minimi digiti; 2. palmar adductor interosseous to the minimus; 3. palmar abducting interosseous of the annularis; 4. palmar adducting interosseous of the annularis; 5. palmar interosseous deviating the medius to the ulna; 6. palmar interosseous deviating the medius to the radius; 7. palmar adducting interosseous of the index; 8. pollical head of the first dorsal interosseous covering the metacarpal of the index; 9. deep head of the flexor brevis pollicis.

Muscles of the Anterior Abdominal Wall.

The *external oblique* arises by well-marked digitations from the outer surfaces and lower borders of ribs 5-11. The mesial

digitations fuse with the pectoralis major, and the outer ones are only covered by the latissimus dorsi. All interdigitate with the serratus magnus. The lateral fibres descend to the anterior superior iliac spine and outer third of Poupart's ligament. The other fibres end in the aponeurosis which is attached to the sternum, the last chondro-sternal junction, the pubis, and the inner two-thirds of Poupart's ligament. The aponeurotic fibres of the two sides cross the mid line into one another. Gratiolet (11) described the aponeurosis in detail, recording the characters of Poupart's ligament, the slight Gimbernat's ligament, the lax adhesion to the deep fascia of the thigh, and the formation of the pillars of the external abdominal ring. The aponeurosis fuses with the internal oblique mesial to the splitting of the aponeurosis of the latter. And the crural fascia and Poupart's ligament fuse with the aponeurotic origin of the sartorius.

The *internal oblique* rises from the outer half of the anterior border of the iliac crest, the anterior superior iliac spine, the outer third of Poupart's ligament, and the lower borders of costal cartilages 10-13. The aponeurosis, which receives the fibres, has a curved line of splitting and runs from the tenth costal cartilage to the inner end of Poupart's ligament.

The *transversalis abdominis* arises from the deep surfaces of ribs 10-13, the lumbar fascia, the anterior quarter of the inner lip of the iliac crest, the inner surface of the anterior superior iliac spine, and the outer third of Poupart's ligament. The aponeurosis is attached to the xiphoid and pubis.

The sheath of the rectus is as in Man, and the semilunar fold of Douglas is present. The *rectus* has two origins, as in Man, but has four inscriptions running right through it to the sheath. *Pyramidalis* is absent.

The *diaphragm* has a comparatively small central tendon receiving muscles arising from ribs 7-13 and interdigitating with the transversalis abdominis, from the back of the sternum by two slips, and from the lumbar vertebræ by the crura and extra slips. The right crus arises as low down as the second lumbar vertebra, and the left one from the first. A slip arises from the transverse process of the second lumbar vertebra and one from the side of the body of the first. The lumbo-costal arches are as in Man.

The *quadratus lumborum* is related to the lumbar fascia as in Man. It arises from the posterior two-thirds of the inner lip of the iliac crest, where it is continuous with the iliacus, and from all the lumbar transverse processes. It is inserted into the inner four-fifths of the last rib and the bodies of the last two dorsal vertebræ.

Muscles of the Pelvic Extremity.

The *psoas parvus* arises by fleshy fibres from the last dorsal and first lumbar vertebræ, and it is connected by a fascial sheet over the *psoas magnus* to the remaining lumbar transverse

processes. Its broad, flat tendon is attached to the ilio-pectineal line close to the emergence of the femoral vessels.

The *iliacus* arises as in Man. It is quite continuous with the *quadratus lumborum*, and it soon fuses with the *psaos magnus*. Its fibres envelop the *psaos* from each side. The *psaos magnus* blends more with the *iliacus* than in Man. It arises from the last dorsal vertebra, the inner inch of the last rib and the bodies and transverse processes of all the lumbar vertebræ. The combined muscle is inserted into the small trochanter and the femoral shaft a little below it. Half of the muscle (mesial part) passes over the ilio-*psaos* tendon and is inserted into the bone posterior to the latter.

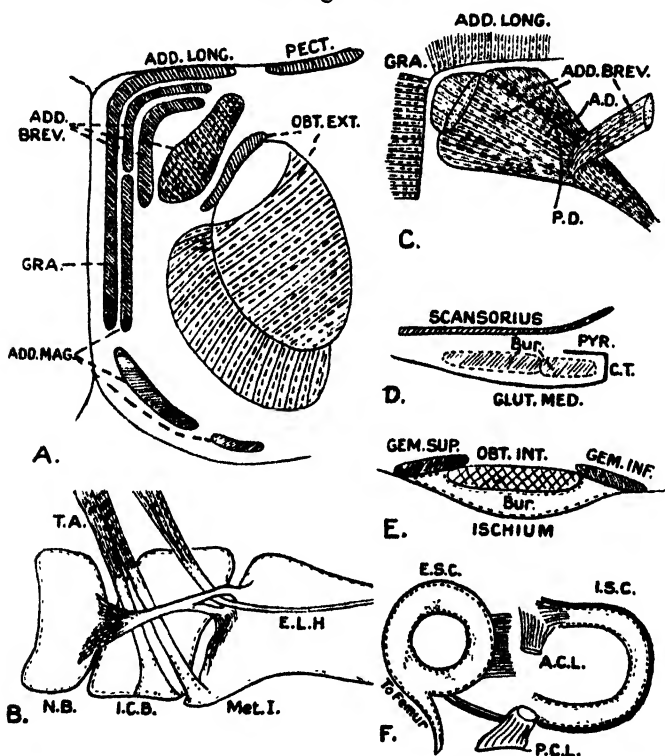
The *sartorius* has a large fan-shaped aponeurotic origin from the anterior edge of the ilium up to a point a finger's breadth below the anterior superior spine. Superficial to the aponeurosis, but connected to it by fascia, is a long, narrow fascial strip connecting the muscle to the anterior superior iliac spine. The strip is connected to the crural fascia and fascia over the abdominal muscles, thus forming a tunnel for the ilio-*psaos*. The comparatively slender muscle is inserted into the upper third of the anterior border of the tibia from the attachment of the ligamentum patellæ downwards. Strong fascia unites it to the inner tuberosity of the tibia and the internal lateral ligament of the knee. Between it and the subjacent *gracilis* is the saphenous nerve, but no bursa.

The *gracilis* and *adductor longus* (text-fig. 36, GRA. and ADD. LONG) arise by a common aponeurosis from the inner end of Poupart's ligament, the entire length of the side of the symphysis, and upper third of the descending ramus of the pubis. No other author describes a precisely similar origin. And the origin conceals the *adductor magnus*. The *adductor longus* occupies the greater part of the aponeurosis, and its fibres approach closer to the bones; it is inserted into the third quarter of the back of the shaft of the femur, and it is fused with the *magnus*. Hepburn (24) describes it as arising by a rounded tendon, and Humphry (26) gives its origin as the spine and inner half of the horizontal ramus of the pubis. The *gracilis* is inserted into the inner aspect of the tibia behind the internal lateral ligament. It is fused with the subjacent *semitendinosus* and the fascia over the inner head of the *gastrocnemius*. Gratiolet (22), Champneys (11), and Hepburn (24) give more extensive origins for a separate *gracilis*.

The *adductor magnus* (text-fig. 36, ADD. MAG) arises by three heads from the pubis and ischium, and it is inserted into the upper three-quarters of the back of the shaft of the femur. The upper head arises from the entire length of the body of the pubis: the middle head from the arch and ischial tuberosity: and the lower head from the tuberosity. The upper and mid heads unite to form a thick muscle inserted into the femoral shaft. The lower head runs separately to the *adductor tubercle*,

and the femoral vessels pass between the two parts to the popliteal space. Champneys (11) reviews the various descriptions. Dwight (10) describes fusion of all the adductors except the part of the magnus to the tubercle. Hepburn (24) states that the latter is really a hamstring, and is supplied by the sciatic nerve. I did not observe fibres from the main mass reaching the knee.

Text-figure 36.



Muscles and joints of the pelvic extremity. A.C.L.: anterior cruciate ligament; C.T.: fibrous connecting slip; E.L.H.: extensor longus hallucis; E.S.C.: external semilunar cartilage; I.C.B.: internal cuneiform bone; I.S.C.: internal semilunar cartilage; Met.I.: first metatarsal bone; N.B.: scaphoid or navicular; P.C.L.: posterior cruciate ligament; PYR.: pyriformis; T.A.: tibialis anticus. Other letters in text.

The *adductor brevis* (text-fig. 36, ADD. BREV) arises by three prismatic, interlocking bellies from the angle between the body and horizontal pubic ramus. Its flat tendon is inserted into a line from the small trochanter to the middle of the back of the femur.

The *pectineus* (text-fig. 36, PECT) arises from the pubic crest on

the three-quarters of an inch internal to the longus. It has a curved insertion running from the lesser trochanter to the back of the shaft of the femur.

Hamstring Muscles:—With the exception of the short head of the biceps, all the hamstrings arise together from the lower and back part of the tuber ischii, and all are fused. The *semitendinosus* is inserted into the anterior tubercle of the tibia, and by a large expansion to the fascia of the leg. The tendon is not as long as in Man (Vrolik and Hepburn), and the insertion is lower. Cuvier showed that this low insertion is incompatible with an erect attitude, and Rolleston pointed out that it occurs in children. The insertion of this muscle, and that of the *semimembranosus* move upwards as the body becomes erect. The *semimembranosus* is smaller than the last muscle, and its long, flat tendon sends no fibres to the fascia over the popliteus, nor to the internal lateral ligament. It is inserted into the tibia over a small area proximal to the other hamstrings. The *biceps* differs somewhat in my specimen from the accounts of Hepburn (24) and Champneys (11). Both heads remain separate. The ischial head has a strong insertion into the outer side of the head of the tibia, the head of the fibula, and the fascia over the outer head of the gastrocnemius. The femoral head is inserted into the head and proximal inch of the shaft of the fibula, and the fascia over the gastrocnemius. It is, therefore, evident that the hamstrings and some of the adductor group are connected to the fascia over the gastrocnemius.

The *gluteus maximus* is smaller than in Man. It arises from the side of the sacrum and coccyx, the great sacro-sciatic ligament and the ischial tuberosity along with the long head of the biceps. No muscle fibres arise from the iliac crest, as in *Phascolarctos*, but it arises from the strong fascia which covers the *gluteus medius*, and is attached to the iliac crest. Hepburn (24) saw it arising from the crest, Humphry (26) observed no fascial origin, and Champneys (11) described conditions similar to mine. The insertion is longer than in Man, for it is fixed to the back of the femur as low down as the external condyle, and to the shaft below the great trochanter. Its fibres mingle with the *vastus externus*. It is fused with the outer head of the *gastrocnemius* (Humphry, 26), and with the *tensor fasciæ femoris* (Wilder, 53).

The *gluteus medius* has a fleshy origin from the whole of the *dorsum illi* down to the line from the great sciatic notch to the anterior inferior spine, and by a dense aponeurosis from the anterior border between the superior and inferior spines. The aponeurosis gives way to muscle after an inch. Fibres also arise from the posterior aspect of the aponeurosis. It is inserted into the top of the outer aspect of the great trochanter. A small slip runs from the mesial aspect of the tendon to join the tendon of the *pyriformis*, thus bringing the two tendons into connection. Two communicating bursæ (text-fig. 36, Bur) separate the

tendons of gluteus medius from those of the scansorius and pyriformis. It is the largest of the glutei. The whole insertion is by closely-set ribbon-like muscles. None of these forms a separated part as described by Champneys (11), but the insertion is split slightly by the vastus externus, as described by Hepburn (24).

The *scansorius* arises from the body of the ilium by a thick muscular origin, and by a thin curved origin from the ilium an inch behind and parallel to the acetabulum. The most external fibres come into relation with the gluteus minimus. It passes over the acetabulum and head of the femur to be inserted into the capsule of the hip from the head to the top of the great trochanter, and to the anterior border of the great trochanter internal to the pyriformis, gluteus medius and vastus externus. It is continuous above with the obturator internus and the gemelli, and below with the gluteus minimus.

The *gluteus minimus* arises from the anterior border of the ilium from the anterior superior spine to below the anterior inferior spine. It is on a slightly more anterior plane than the scansorius. Its insertion is linear and continues that of scansorius downwards for a centimetre. The insertion is covered by the vastus externus.

The *tensor fasciæ femoris* arises from the back of the iliacus, and is inserted into the fascia of the leg more than half-way down the leg. Some authors have stated that the scansorius corresponds to the tensor fasciæ, and others describe only the former. Champneys (11) describes both.

The *gemellus superior* (text-fig. 36, GEM.SUP) arises from a small area on the outer surface of the ischial spine, and from the attachment of the lesser sacro-spinous ligament above the groove for the tendon of the obturator internus. The *gemellus inferior* (text-fig. 36, GEM.INF) arises within the pelvis from a linear origin, and from the top of the outer aspect of the tuber ischii below the groove for the tendon of the obturator internus. The *tendon of the obturator internus* (text-fig. 36, OBT.INT) formed by a fusion of fascicles, is separated from its groove in the ischium by a bursa. It is overlapped by the gemelli which fuse over it. They all have a common insertion into the femur above the trochanteric pit. It is intimately connected to the capsule of the hip joint. Between the hip joint and the tendons of obturator internus and gemelli and the quadratus femoris and obturator externus there is a pad of fat. Hepburn (24) states that the gemellus superior is less than the inferior, and it is difficult to separate the latter from the quadratus femoris, but that is not the case in this animal. Champneys (11) agrees with me in the relative sizes of the gemelli.

The *quadratus femoris* arises from the inferior ramus and upper edge of the tuber ischii above the origin of the hamstrings. It has an angular insertion into the lower part of the inter-trochanteric crest and lesser trochanter, and then horizontally

outwards for an inch into the upper end of the insertion of the adductor brevis.

The *obturator externus* (text-fig. 36, OBT.EXT) arises by two heads. The large head arises from the inferior ramus of the pubis between the obturator foramen and the origins of the adductor magnus, and from the obturator fascia. The small head arises from the horizontal ramus of the pubis between the obturator canal and origin of the lateral head of the adductor brevis. The two heads unite, and the tendon is inserted into the trochanteric pit and capsule of the hip joint.

There is greater connection between these muscles, and the capsule of the hip joint is considerable.

The *rectus femoris* arises by two heads which, however, are not very distinctly separate. The straight head arises from the anterior aspect of the ilium between the anterior inferior spine and the acetabulum. The reflected head forms an arch over the whole of the upper part of the acetabulum, and the upper fibres are connected by a dense aponeurosis with the iliacus. The *vastus externus* arises from a small area on the antero-lateral aspect of the great trochanter below the insertion of the scanorius, whose tendon it splits. The origin is continued down on the back of the femur, anterior to and continuous with the gluteus maximus, to an inch above the external condyle. A small part, arising from the anterior part of the bone below the great trochanter, is at first separated from the main mass by the gluteus minimus. And an additional slender belly springs from the upper end of the intertrochanteric line. The *vastus internus* arises from the intertrochanteric line except its extreme upper end. And it springs from the back of the femur down to a point an inch above the internal condyle. The *crureus* arises from the upper two-thirds of the surface of the femur between the two vasti. The *quadriceps extensor tendon* is wide and receives the muscles an inch above the patella. It is attached to the upper border of the patella, the capsule of the joint on either side of it, the internal condyle of the tibia, and the outer femoral and tibial condyles. The ligamentum patellæ is inserted into the front of the upper end of the tibia. No *subcrureus* is present.

Tibialis Anticus:—Macalister (33), Hepburn (24), Champneys (11), and others have described double origins and insertions. The insertions are into the entocuneiform and first metatarsal. Wilder (53) points out that the double insertion is in accord with the use of the hallux as a thumb. In this animal the origin is from the outer aspect of the outer condyle and the upper half of the outer aspect to the tibia, from the middle third of the delicate interosseous membrane, from the fascia between it and the extensor longus digitorum, and from the fascia over it. The lateral superficial fibres form the superficial belly of the muscle, which is inserted into the base of the first metatarsal bone. The other fibres form the deep belly, which runs to the internal cuneiform (text-fig 36 B). The superficial belly has a mucous

sheath almost to its insertion; but the deep belly loses its sheath on the dorsum of the foot, and is separated from the cuneiform bone by a bursa.

The *extensor longus digitorum* arises from the external condyle of the tibia internal to the head of the fibula, the anterior border of the head of the fibula, the antero-medial surface of the fibula to within an inch of the malleolus, the anterior peroneal inter-muscular septum to the same level, the fascia between it and the tibialis anticus and the fascia over its upper half. The belly passes through the lateral compartment under the annular ligament, and divides into four slips. The second slip is thready, but the others are well developed. The first slip divides into two; the medial one going to the dorsum of the second toe, and the lateral one joins the second slip and runs to the third toe. The third and fourth slips run to the fourth and fifth toes. The slips form dorsal expansions over the metacarpo-phalangeal joints and proximal phalanges, which are joined by the lumbricales, interossei, and extensor brevis, except in the case of the fifth toe. The actual insertions into the bones are as in Man.

The *extensor longus hallucis* arises from the middle third of the antero-medial surface of the shaft of the fibula, and from the outer part of the interosseous membrane, posterior to the extensor digitorum longus. The belly passes through the middle compartment under the anterior annular ligament, and continues as a tendon round the inner surface of the entocuneiform. It runs through the naviculo-metatarsal trochlea (text-fig. 36 B) and reaches the dorsum of the metatarsal of the hallux. A dorsal expansion is formed over the first phalanx, the proximo-lateral part of which joins the tendon of insertion of the most medial tendon of the extensor brevis digitorum. The rest of the tendon has an expanded insertion into the base of the terminal phalanx of the hallux and the capsule of the interphalangeal joint.

The *peroneus tertius* is absent.

The *gastrocnemius* has two heads, but they arise more posteriorly and distally than in Man, and from the capsule of the knee joint instead of from bones. They spring from the capsule over the articular surface. They are inserted into a median tendinous raphé, the inner belly slightly overlapping the external, and extending more laterally. The flattened tendon joins the tendon of the soleus, half an inch above its insertion into the calcaneus, forming the tendo Achillis. The edges of the muscle are firmly connected to the subjacent soleus.

The *plantaris* arises lower down than in Man, from the postero-lateral side of the external femoral condyle. The slender belly, three inches long, passes under the lateral belly of the gastrocnemius, and the very fine thread-like tendon has an expanded insertion into the tendo Achillis close to the calcaneus.

The *soleus* has no tibial origin, and is smaller than in Man. It has a fleshy origin from the posterior aspect of the head of the fibula, and an aponeurotic origin from the upper part of the

peroneal intermuscular septum. The flat belly gradually expands till it reaches a point an inch above the calcaneus. The superficial part of the central portion becomes tendinous in the lower third, and is joined by the gastrocnemius to form the tendo Achillis. The tendo Achillis is inserted into the middle of the posterior aspect of the os calcis. It is separated from the upper part of the bone by a bursa and a pad of fat.

The *popliteus* is double, but its origins and insertions are all in contact to form linear attachments. The proximal fibres rise from the posterior aspect of the capsule of the knee-joint internal to the outer head of the gastrocnemius. The distal fibres arise as in Man. The proximal part is inserted into the vertical line on the posterior aspect of the internal tibial condyle. The distal part goes to the oblique popliteal line, the posterior border of the subcutaneous area, the internal condyle and a curved line running round the internal condyle.

The *flexor longus digitorum* arises from the popliteal line and its medial continuation downwards to within half an inch of the inner malleolus, and from the septum between it and the tibialis posticus. The tendon passes round the back of the internal malleolus and under the inner end of the internal annular ligament. It crosses to the lateral side of the sole of the foot and is joined by the tendon of the accessorius and a slip from the flexor longus hallucis. A small slip runs to the lateral tendon of the flexor brevis digitorum. Then it divides into five tendons for the four inner toes, the fourth receiving two. The first and second tendons, to the second and third toes, are accompanied superficially by tendons of the flexor brevis. In the case of the fourth toe the superficial tendon of the longus replaces the tendon of the brevis. The tendons are inserted as in Man. The tendon to the little toe is attached by a broad vinculum to the body of the proximal phalanx, by a triangular vinculum to the second phalanx and is inserted into the base of the terminal phalanx. The flexor sheaths are as in Man.

The *four lumbricales* pass to the inner parts of the dorsal expansions of the extensor tendons of the four inner toes.

The *accessorius* is very small and has only the external head which runs from the outer edge of the calcaneus and the long plantar ligament to the outer aspect of the flexor longus digitorum.

The *flexor longus hallucis* arises from the lower part of the posterior aspect of the head of the fibula, from the posterior surface of the fibula almost to the malleolus, from the fascia between it and the tibialis posticus, from the posterior peroneal intermuscular septum, the lower part of the interosseous membrane and slightly from the tibia near the interosseous membrane. The tendon is inserted into the base of the terminal phalanx of the hallux, and the capsule of the interphalangeal joint. In the sole a large tendon connects it to the flexor longus digitorum. It has a flexor sheath. The tendon runs through a trochlea attached to the base of the first metatarsal.

The *tibialis posticus* arises from the lower part of the head and upper part of the body of the fibula anterior to the flexor longus hallucis, from the upper half of the interosseous membrane, the upper half of the tibia external to the popliteal line and its downward continuation and from the septum between it and the long flexors. It is inserted much as in Man, only the scaphoid here has no definite tubercle.

The *peroneus longus* arises from the anterior half of the outer surface of the head of the fibula, the antero-lateral surface of the fibula to within an inch of the malleolus, the upper half of the anterior peroneal septum, the posterior peroneal septum and the fascia over it. The tendon passes behind the outer malleolus and external to the peroneus brevis, and from there on it is as in Man.

The *peroneus brevis* arises from the lower half of the antero-lateral surface of the fibula down on to the lateral malleolus, the anterior peroneal septum and the fascia over it. The tendon goes behind the outer malleolus and is inserted into the projecting base of the fifth metatarsal. An inch below the malleolus the tendon gives a slip to the dorsal expansion on the dorsum of the proximal phalanx of the fifth toe.

The *extensor brevis digitorum* arises from the outer side of the upper surface of the os calcis anterior to the posterior facet, the dorsal calcaneo-cuboid ligament and the lower border of the external annular ligament. Its four fleshy bellies end in slender tendons to the four inner toes. The most medial tendon has an expanded insertion into the base of the dorsum of the proximal phalanx of the hallux. The other three join the dorsal extensor expansions, thereby being inserted into the bases of the second and third phalanges.

The *flexor brevis digitorum* arises as in Man. It divides into two tendons, the lateral one to the third toe being joined by a slip from the long flexor. The medial one goes to the second toe. Insertion as in Man.

The *abductor hallucis* arises as in Man, and it also receives fibres from the inner side of the foot (internal annular ligament, scaphoid, entocuneiform and capsule of the metatarso-phalangeal joint). It is inserted into the inner aspect of the capsule of the first metatarso-phalangeal joint and the base of the first phalanx, with the interposition of a sesamoid bone. A small slip passes to the shaft of the first phalanx.

The *abductor minimi digiti* arises as in Man. It is inserted into the outer side of the projecting base of the fifth metatarsal (abductor ossis metatarsi quinti of Hepburn), the inner side of the base of the fifth metatarsal, the outer side of the plantar aspect of the capsule of the metatarso-phalangeal joint and base of the proximal phalanx, and the outer side of the shaft and the dorsal expansion on the first phalanx. Hepburn (24) mentions the latter in the Orang.

The *flexor brevis hallucis* has two bellies. The deep inner one

arises from the entocuneiform, the sheath of the peroneus longus tendon, the capsule of the first metatarso-phalangeal joint, and the lower half of the outer border of the first metatarsal. The outer belly arises from the sheath of the peroneus longus and the external long plantar metatarsal ligament where it is attached to the outer surface of the base of the fourth toe. No fibres arise from the cuboid. The two bellies together with the two adductores hallucis are inserted into the outer side of the base of the first phalanx of the hallux and the capsule of the joint with the interposition of a sesamoid. The internal head is really a first interosseous.

The *adductor obliquus hallucis* arises from the base of the third metatarsal and the proximal half of the external long plantar metatarsal ligament. The *adductor transversus hallucis* arises from the upper half of that ligament and from the internal long plantar metatarsal ligament, and the capsules of the second and third metatarso-phalangeal joints.

The *flexor brevis minimi digiti* arises from the plantar aspect of the fifth metatarsal bone and the sheath of the tendon of the peroneus longus. It is inserted into the capsule of the fifth metatarso-phalangeal joint and outer side of the base of the proximal phalanx.

The *opponens minimi digiti* arises from the proximal half of the plantar surface of the fifth metatarsal and the sheath of the peroneus longus. It is inserted into the inner side of the capsule of the metatarso-phalangeal joint. There are four dorsal and three plantar *interossei*, but Dwight (18) mentions a large number. The four dorsal *interossei* arise as in Man; but their insertions differ in that they abduct from a line drawn through the middle toe. This resembles the arrangement in the hand, but not in the human foot where the mid line runs through the second toe. Hepburn (24) records the line as resembling that in the human foot, but Champneys (11) and Cunningham (13) point out that in all Primates except the Gorilla and Lemur the *interossei* abduct the toes from a line through the middle one. The attachments of the dorsal *interossei* are as follows:—

No. 1 inserted into the inner side of the second digit.

2	"	"	"	"	"	"	"	third	"
3	"	"	"	outer	"	"	"	"	"
4	"	"	"	"	"	"	"	fourth	"

The three plantar *interossei* adduct towards the middle toe instead of the second as in Man. The first arises in the second interspace from the whole length of the outer side of the second metatarsal, and a few fibres arise from the base of the third metatarsal, as Hepburn (24) finds in the Gorilla. It is inserted into the outer side of the second toe. The second arises from the inner side of the fourth metatarsal and the ligamentous structure covering the bone. It is inserted into the inner side

of the same toe. The third is placed more superficially than the others, and lies in the same plane as the *opponens minimi digiti*. Its belly crosses the fourth space from its origin on the external long plantar metatarsal ligament, and the ligaments over the base of the fourth metatarsal to its insertion on the inner side of the fifth toe.

The dorsal interossei are inserted more into the proximal phalanx than into the dorsal expansion, but the plantar interossei exhibit the reverse.

The important points to be noted from the physiological point of view are:—1. The middle line of the foot runs through the middle toe instead of through the second, as in Man. So the interossei of the foot of the Chimpanzee act as they do in a hand. 2. There are no additional plantar interossei in the foot as there are in the hand.

The disposition of the muscles in four layers in the sole of the foot is as in Man.

The nature of the terminal part of the pelvic extremity is described on page 423.

Muscles of the Pelvis.

Levator Ani:—In this animal the levator ani consisted of the same parts as described by Lartschneider (32). The iliac portion arose from the margin of pelvis minor, and the pubic portion arose from the back of the symphysis pubis. It is inserted into the sides of the lower end of the rectum and the ano-coccygeal raphé.

The *ischio-coccygeus* is a small muscle running from the side of the coccygeal vertebræ to the inner aspect of the back part of the ischial tuberosity.

Lartschneider has described a pelvic diaphragm in a female Chimpanzee.

The *perineal muscles* differ from those in the human condition. The vulva and anus are very close together, so there is no true central point of the perineum, nor is there a trace of transverse perineal muscles. The *ischio cavernosi* have long origins from the ascending pubic rami; they run over the crura clitoridis, and the opposite muscles are blended. The *sphincter vaginae* is a strong collar surrounding the upper part of the vagina and extending backwards on to the rectum. It has a narrow anterior slip which fuses with the meeting point of the two *ischio-cavernosi*. The *sphincter ani externus* blends in front with the *sphincter vaginae*, and is attached behind to the ano-coccygeal raphé, which is very powerful.

The ischio-rectal fossæ are well marked and laden with fat. No well-marked bursa exists over the ischial tuberosities. And the fascia is not divided as in Man into a superficial fatty layer and a deep fascia of Colles.

The orbital muscles are described on page 415, and the laryngeal muscles on page 398.

THE JOINTS.

Spinal Ligaments:—The *anterior common ligament* extends from the axis to the upper segment of the sacrum, and is smaller above than below. It is attached to the front of the centra, but not to the depressions between the vertebræ. The *supraspinous ligaments* run as in Man, and are connected to interspinous ligaments. There is no *ligamentum nuchæ*. The *interspinous ligaments* are as in Man. The *ligamenta subflava* run from the anterior aspect of the lamina above to the posterior aspect of the lamina below. They and the interspinous ligaments are very elastic. The *posterior common ligament* runs from the axis to the sacrum, but is not so dentate in appearance as in Man. It is narrow on the centra, and expanded over the intervertebral discs.

Costal Articulations (text-fig. 37 A & B):—Anteriorly the head of the rib is connected by a fan-shaped ligament, not divisible into three parts as it is in Man, and the fibres all gain attachments to the anterior common ligament (A.C.L). The upper fibres run to the vertebra above, and the lower ones to the vertebra below, where they are overlapped by the upper fibres of the next joint. Posteriorly the tubercle of the rib is attached to the transverse process of the vertebra by a capsule. The upper border of the neck of the rib is connected to the transverse process by a fan-shaped ligament (C-T.L.).

The *intertransverse ligaments* (I-T.L.) are fan-shaped. They connect the tip of the transverse process above to the upper border of the transverse process below.

The lengths of the spinous processes of the cervical vertebræ are:—axial $\frac{5}{8}$ inch; 4th vertebra $\frac{3}{4}$ inch; 6th and 7th vertebræ $\frac{7}{8}$ inch.

Atlanto-axoid Joints:—The posterior atlanto-axoid ligament, from the posterior arch of the atlas to the upper border of the axis, corresponds to the *ligamenta subflava* elsewhere. It is strengthened by fibrous bands (text-fig. 37, F.B): *a*. From the transverse process of the axis to an elevation on the posterior arch of the atlas; *b*. A central atlanto-axoid band (C.A.B); *c*. Several small bands between the others. The *anterior atlanto-axoid ligament* is a very strong band continuing the anterior common ligament from the axis to the atlas.

Joints of the Occipital, Atlas, and Axis (text-fig. 37 D):—The *posterior occipito-atlantoid ligament* is a thin membrane running between the posterior arch of the atlas and the edge of the foramen magnum. It is strengthened by lateral bands, attached close to the condyles. It functions as a posterior capsular ligament. An internal capsular ligament runs from the inner border of the condyle to the superior articular process of the atlas. And a strengthening band runs from the posterior arch of the atlas to the occipital bone close to the attachment of the internal capsular ligament. The *anterior occipito-atlantoid*

ligament is a strong membrane continuing the atlanto-axoid ligament from the anterior arch of the atlas up to the anterior half of the circumference of the foramen magnum. The *membrana tectoria* continues the posterior common ligament up to the cranial surface of the basi-occiput where it spreads out in a fan-shaped manner. The *posterior occipito-axoid ligament* (P.O.-A.L) is a strong band on each side on the deep aspect of the *membrana tectoria*. It extends from the antero-lateral part of the vertebral canal to the basi-occiput. It passes lateral to the odontoid process and covers the spinal aspect of the lateral part of the transverse ligament and conceals it from view. The *transverse ligament* (T.L) is a strong band running behind the odontoid process. It is attached by its extremities to the inner aspect of the inferior atlantic articular processes. The *cruciate ligament* has no inferior crus. The superior crus (S.C.C) is broader and shorter than in Man. It runs from the transverse ligament below to the basi-occiput below the *membrana tectoria* above. The *check ligaments* (C.L) are more horizontal than in Man. They run from the odontoid to the inner aspect of the occipital condyles. The *middle odontoid ligament* runs from the tip of the odontoid to the anterior edge of the foramen magnum. It is stronger and more horizontal than in Man. *Capsular ligaments* are as usual. As the odontoid runs farther upwards than in Man the ligaments are modified.

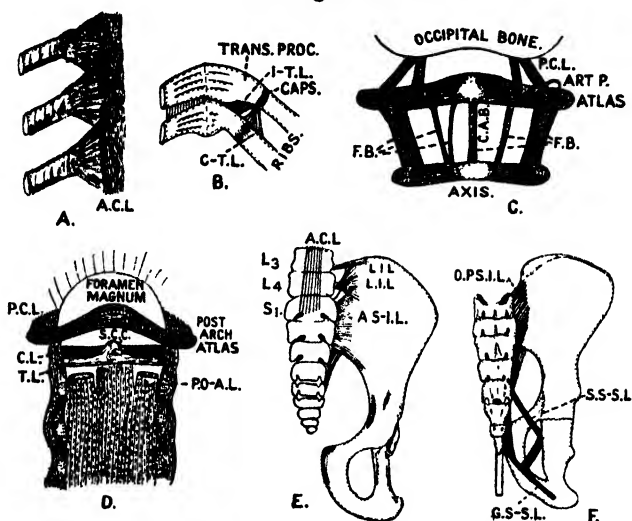
The lumbar vertebræ are connected by the usual capsular ligaments, intervertebral discs and ligaments connecting their processes.

Ligaments of the Pelvis (text-fig. 37):—The lumbar vertebræ are included more closely between the ilia than in Man, and the pelvic ligaments differ in several respects. The *lumbo-inguinal ligaments* (L-I.L) consist of an upper horizontal ligament running from the third lumbar transverse process to the inner lip of the crest of the ilium, and a lower fan-shaped one from the fourth lumbar transverse process to the inner lip and inner surface of the ilium. The fibres of these ligaments are continuous; and the lower one is continuous with the *anterior sacro-iliac ligament* (A.S-I.L). The latter is fan-shaped, and runs from the ala sacri to the anterior surface of the ilium, where it spreads out in a fan-shaped manner. Some fibres run along the pelvic brim. The *short posterior sacro-iliac ligament* is as in Man. It is superficially thickened to form the *oblique posterior sacro-iliac ligament* (O.P.S-I.L), which runs from the posterior tubercles of the sacrum to the two posterior iliac spines and the bone between. The *great sacro-sciatic ligament* (G.S-S.L) runs from the side of the lower sacral and upper coccygeal vertebræ. It narrows and then it expands again on the posterior part of the inner aspect of the ischial tuberosity. A falciform process runs forwards to become the sub-pubic ligament. The ischial spine is slight, but it receives a broad expansion from the great sacro-sciatic ligament, and a cord-like *small sacro-sciatic ligament*

(S.S.-S.L) from the side of the lower end of the sacrum. It can be seen from text-fig. 37, that the pelvic outlet is divided into seven parts by ligaments. The *obturator membrane* is dense and strong. The *symphysis pubis* has the same ligaments as in Man. The upper and sub-pubic ligaments are weak, but the anterior and posterior ones are strong, particularly the latter. Within the inter-articular cartilage there is a small synovial cavity.

The *Temporo-maxillary Joint* :—The *capsule* is thick and strong, the upper part of its outer surface giving origin to some of the deeper fibres of the *masseter*. The *synovial cavity* is divided into two by an articular disc which, however, is not perforated.

Text-figure 37.



Ligaments of the spinal and pelvic joints. ART.P: articular process; CAPS: capsules; P.C.L.: posterior capsular ligaments. Other letters in text.

The disc is much thicker behind than in front, and lies closely on the condyle of the mandible, moving with it in mastication. It is concavo-convex from before backwards on its upper surface. *Posterior temporo-mandibular* and *external lateral* ligaments are present, the latter being very strong. The inner aspect of the capsule is thin. The *internal temporo-mandibular ligament* is small, but definite, and blends with the capsule. The anterior aspect of the capsule is covered by the insertion of the external pterygoid. The *spheno-mandibular ligament* is very poor.

The *acromio-clavicular joint* is as in Man.

The *Shoulder Joint* :—The shoulder joint is in many ways as in Man, but the following points deserve special mention. The

subscapular bursa opens into the joint cavity above the superior gleno-humeral ligament. The *coraco-humeral ligament* blends with the capsule near the insertion of the subscapularis. The *coraco-acromial arch* is a strong band, and there is also a weak *acromio-humeral ligament*. The insertions of the supraspinatus and infraspinatus are most intimately blended with the capsule, and cannot be separated from it. The posterior part of the capsule is weak and loose, but the anterior part contains a broad, powerful *anterior gleno-humeral ligament*. The capsule is attached to the bones as in Man. The *superior gleno-humeral ligament* divides into two parts, which are inserted separately into the humerus, and the subscapular bursa communicates with the joint between them. The cotyloid ligament and tendon of the biceps are as in Man.

The *Elbow Joint*:—The posterior part of the *capsule* is attached as in Man; and a strong band passes from the tip of the olecranon up to the outer part of the olecranon fossa, which contains fat. The anterior part of the capsule is relatively strong all over. On the radial side the fibres run downwards and inwards, but those on the ulnar side run downwards and outwards. The fibres of these sides interlace and make the capsule strong. The *internal lateral ligament* is very strong. It arises from the internal condyle and spreads out to be attached to the whole inner margin of the olecranon, the coronoid and the great sigmoid notch. The thickest parts are fixed to the olecranon and coronoid, but it has no transverse part. The *external lateral ligament* is attached as in Man. It is weaker than the internal ligament, but muscles arise from it.

The *Superior Radio-Ulnar Joint*:—The capsule of the elbow joint is prolonged down for $\frac{3}{4}$ inch over the head and neck of the radius. The orbicular fibres are as in Man, but there is no oblique cord. The *interosseous ligament* begins at the lower part of the coronoid process. One set of fibres runs downwards and outwards to be inserted into the radius below the bicipital tuberosity. A second group runs from the insertion of the first to the ulnar interosseous border; it is by far the stronger group, and lies anteriorly.

The *Synovial Cavity of the Elbow Joint*:—This is attached to the margin of the coronoid fossa, but more superiorly than the fossa for the head of the radius. The line of attachment then passes about half-way between the articular surfaces and the condyles. On the posterior surface the capsule is attached round the margin of the olecranon fossa. On the radial side the attachment corresponds to a line joining the epicondyles and drawn on the part of the humerus which articulates with the radius. On the ulnar side it is attached to the margin of the olecranon fossa, greater sigmoid notch and coronoid, but it jumps the gap between the margins of the lesser sigmoid notch, where it gives rise to orbicular fibres.

The *Wrist Joint*:—The anterior and posterior aspects of the carpus are covered by bands of fibres running in all directions; but

there is no centre of radiation as in Man. The following thickened bands deserve mention:—(1) A strong band from the anterior aspect of the base of the radial styloid to the trapezium and os magnum; (2) a weak *external lateral ligament*; (3) a small *internal lateral ligament*; (4) a thickened band from the posterior part of the distal radio-carpal joint to the back of the os magnum; (5) a posterior band from the distal part of the radius to the cuneiform and unciform bones. Both anterior and posterior ligaments are stronger than in Man. The *cavity of the joint* (text fig. 35 B) is complicated. The distal end of the radius is divided into two facets, which articulate with the scaphoid and semilunar bones. No articular fibro-cartilage lies on the distal end of the ulna, but a very strong ligament runs from the distal end of the ulna to the proximal end of the pisiform bone. It plays over the outer aspect of the ulnar styloid, which is covered with cartilage. The synovial cavity between the radius and the scaphoid and semilunar bones is prolonged into the inferior radio-ulnar joint, over the ulnar styloid and ligament and upon the surface of the cuneiform bone; it gets in between the cuneiform and pisiform. A large cavity separates the head of the os magnum from the concave surfaces of the scaphoid and semilunar bones, and it also separates the cuneiform and unciform. It is continuous with the cavity between the scaphoid and trapezoid. A small ligament connects the scaphoid and os magnum and divides the cavity partially into inner and outer parts. This transverse carpal cavity is prolonged distally on either side of the os magnum. Two interosseous ligaments are also present in the joint. A sesamoid bone lying on the apex of the pisiform is separated from it by a synovial cavity and a strong interosseous ligament.

Carpo-metacarpal Joint:—A continuous cavity extends along the proximal ends of metacarpals 2-5. It is connected with the transverse carpal cavity (text-fig. 35). Two interosseous ligaments run from the os magnum to the sides of the third metacarpal bone. In the *intermetacarpal joints* there are prolongations of the carpo-metacarpal synovial cavity, and interosseous ligaments connect the second to fifth metacarpals to one another. The *metacarpo-phalangeal joints* are as in Man, but the dorsal expansions of the extensor tendons can easily be separated from the capsules. The *inter-phalangeal joints* are as in Man. Their internal and external lateral ligaments are powerful.

Pollical Joints:—A prolongation of the transverse carpal cavity runs between the scaphoid and trapezium, and between the trapezium and trapezoid, where there is also an imperfect interosseous ligament. A strong ligament runs from the trapezium to the base of the index metacarpal. The carpo-metacarpal capsule is complete; it is thick and strong on its outer and posterior aspects, but its inner and anterior aspects are weak. The metacarpo-phalangeal and interphalangeal joints are as in Man, and in the other digits of the Chimpanzee.

The *Hip Joint*:—The capsule is attached as in Man. The *ilio-femoral ligament* consists of one band, which arises under cover of the rectus femoris and is strengthened by its tendon. It runs as does the anterior band of the Y-shaped ligament in Man. No other ligaments are formed from the capsule. The gluteus minimus strengthens the capsule at the proximo-anterior part of the great trochanter. The ligamentum teres, cotyloid ligament, and transverse ligament are as in Man. The joint contains a pad of fat.

The *Knee Joint*:—The *ligamentum patellæ* is broad and strong, and has a more extensive insertion than in Man (see page 358). The *internal lateral ligament* is not inserted into the internal condyle of the tibia, but is fixed to the upper third of the shaft. The *external lateral ligament* is as in Man. The *oblique popliteal ligament* is absent, but a strong femoral intercondylar ligament is attached to the posterior aspects of the two condyles. The *ligamentum mucosum* is just as in Man. The *anterior cruciate ligament* is attached to the tibia as in Man, but its femoral insertion is into the upper half of the mesial aspect of the external condyle. It is smaller than the *posterior cruciate ligament*; the latter is attached to the tibia farther back than in Man, and it receives a slip from the external semilunar cartilage (text-fig. 36 F). Two *semilunar cartilages* are present. The internal one is larger than the external, and is crescentic in shape. It is attached in front of the anterior cruciate ligament. Its posterior horn is inserted as in Man. The external cartilage forms a small, complete circle. Internally it is attached by a broad ligament to the external side of the tubercles and spine of the tibia. Postero-mesially it is united by a ligament to the outer surface of the internal condyle of the femur. It is also connected to the posterior cruciate ligament. The joint differs in many ways from that in Man, and its construction is such that it is one of the factors which prevent the animal assuming a firm, erect attitude. Humphry (26), who has made a thorough study of this joint, points out that the femur in Man is broad and comparatively flat on the distal end of the external condyle; and the attachments of the lateral ligaments are nearer the posterior parts of the bone. So the joint is firm and locked when it is fully extended. In the Chimpanzee, on the other hand, the distal end of the external condyle is rounded, and the lateral ligament is not attached far back. He also shows that the lateral, cruciate, and posterior ligaments are all tight when the human knee is fully extended, but they never become simultaneously tight in the Chimpanzee; to obtain tightness of each ligament it is necessary to divide all the others. Finally, the attachment of the gracilis and hamstring muscles to the fascia of the leg, and the laxity of the ligaments of the joint, are contributory factors which prevent the animal assuming the erect attitude*.

* See the observations on living specimens recorded on page 420.

The *Ankle Joint*:—The capsule is attached above to the distal ends of the tibia and fibula and below to the astragalus. A small *deltoid ligament* runs from the medial and distal border of the tibia to the sustentaculum tali and talus. Posteriorly a very strong *fibular calcanean ligament* is present; and it is strengthened by an accessory ligament from the lateral aspect of the lower end of the fibula. A *tibial calcanean ligament* lies on the inner aspect of the joint. The *talo-fibular ligaments*, both anterior and posterior, are present, but the former is ill-defined. A ligament runs from the middle of the anterior distal border of the tibia, under the talus, to the medial aspect of the lateral distal tubercle of the calcaneus. The tibia and fibula are held together by thin membrane. The *talo-calcanean ligaments* are well-developed. The dorsal, posterior, and two lateral ones are strong, but the medial one is weak. The posterior ligament takes part in forming an interosseous ligament. The talus is further held in position by a ligament running from the plantar navicular-calcanean ligament to a small impression on the head of the talus.

Ligaments connected with the Calcaneus:—The plantar calcaneonavicular ligament runs from the sustentaculum tali to the navicular; and there is practically no internal ligament between these bones. A well-marked ligament connects the calcaneus and cuboid.

The *long plantar ligament* is attached proximally to the cuboid, and distally to the bases of the second, third, and fourth metatarsal bones. No short plantar ligament exists.

A fine ligament attaches the cuboid to the lateral extremity of the base of the fifth metatarsal, and another connects it to the third cuneiform.

Navicular Ligaments:—A dorsal ligament runs from the navicular bone to the base of the second metatarsal, and a medial ligament connects it to the first cuneiform.

An interosseous ligament holds the cuboid and cuneiforms in position.

Plantar Metatarsal Ligaments:—The external ligament is an aponeurotic septum attached obliquely to the fourth metatarsal from the outer side of the base across the plantar aspect of the shaft to the head. The adjacent parts of the bases of the third and fourth metatarsals are covered by ligamentous fibres from the sheath of the tendon of the peroneus longus, and representing the termination of the long plantar ligament. This divides into two strands, the external one joining the external ligament, and the internal one passing along the whole length of the third metatarsal as the internal long plantar metatarsal ligament.

Humphry (26) has gone very fully into the shapes of the bones of the foot and the part played by the bones, ligaments, and muscles in its mechanics. He draws attention to the following points:—(1) The shape of the talus throws the weight on the outer

border of the foot; (2) the talus and calcaneus are more for progression than support; (3) the calcaneus easily rolls outwards on its lower surface, so does not act as a bearing surface; (4) the calcaneus is thrown out of the plane of gravity, and it is reduced like its homotype, the pisiform, to a lever for muscles; (5) the talus, navicular, and calcaneo-navicular ligament transmit weight; (6) the posterior surface of the talus slopes downwards and inwards; (7) the action of the calf-muscles on the foot is unfavourable for lifting weight or propelling the body; (8) there is no plantar arch, so the navicular bone with the calcaneo-navicular ligament rest on the ground and do not transmit weight along the arch to the hallux, which is not adapted for support; (9) the mobility of the hallux is obtained by articular, osseous, and muscular arrangements similar to those of the human pollex; (10) there is more power of flexing the digits towards the sole than in Man.

It is, therefore, evident that the joints of the neck, pelvis, wrist, and lower extremity, particularly the latter, differ considerably from those in Man, and all are specialisations in accordance with the mode of locomotion.

THE ORGANS OF DIGESTION.

The loose, thick, fleshy *lips* are projected forwards over the maxillæ. No philtrum is present, and in the living animal only a small part of the red margin of the lower lip is visible when the mouth is closed. Their inner surfaces are studded with the openings of numerous labial salivary glands. The labial frenula are long and narrow. The gape of the mouth is wide. The *cheeks* are loose and mobile, but no pouches exist. The *vestibule* is semilunar, and receives the secretions of Stensen's ducts, which open on papillæ placed as in Man. And a row of papillæ lies beside the salivary papilla on each side (text-fig. 28 C). Rex (41) has described the histology of the lips, and Ehlers (59) described folds of mucous membrane connecting the gums and cheeks. The *cavum oris* is thrice as long as broad according to Gratiolet (22). In my specimen the measurements are:—

Length of hard palate.....	2·7 inches.	
Length of soft palate	1·1 ,,	Total=3·8 inches.
Greatest width of palate...	1·4 ,,	

Much, however, depends on the age of the animal. Keith has shown that the breadth of the palate is greater than the length in new-born animals. The cavity of the mouth has also been mentioned by Symington (48) and Tyson (50).

The rugæ of the *hard palate* have been figured or described by Beddard (3), Bischoff (60), Ehlers (59), Gratiolet (22), Symington (48), and Waldeyer (52). In my specimen there are no complete ridges crossing the palate, and no incisive papilla. Eleven pairs

of ridges radiate from the median raphé, which is thicker anteriorly than posteriorly. The *soft palate* has the same histological structure as in Man, and its glands are very numerous. Using C. for complete ridges, I. for incomplete ridges, P. for incisive papilla, R. for median raphé, and U. for uvula, the formula is C0, I11-11, P0, R+, U+.

In a former paper (46) I described the *tongues* of several specimens, and I collected the literature. In this animal there are eight papillæ arranged in a Y.

The *pharynx* is as in Man. Fauical and pharyngeal tonsils are both present, and are nourished from the vascular circle formed by the branches of the ascending pharyngeal artery (text-fig. 29). The former is covered by fenestrated mucous membrane. Although lingual, faucial and pharyngeal tonsils are present I was unable to detect Waldeyer's lymphatic ring. Seessel's pocket is absent. The constrictor muscles are as in Man. The sinus of Morgagni is large, and the levatores and tensores palati are more horizontal owing to the prognathism of the skull than in Man.

The *œsophagus* is entirely behind the trachea in the neck. It has similar relations in the neck and thorax to those in Man. The mucous membrane is thrown into prominent longitudinal folds in the cervical and thoracic parts, but the former are more numerous and closer together. The walls are thinner and more dilated in the lower part of the *œsophagus*. In the upper part the inferior constrictor joins the outer longitudinal muscular coat of the *œsophagus*, which increases in thickness from above downwards, and becomes continuous with the outer coat of the gastric musculature. The circular muscle coat thickens from above downwards and also becomes continuous with the circular fibres of the stomach. At the lower end of the *œsophagus* it forms the sphincter of the cardia, which is two inches long. The inner longitudinal fibres in the upper part consist of a few strands, and the submucosa bulges between them; they are entirely absent in the lower part of the *œsophagus*. Man has only two muscular coats.

Cunningham (14) has given a fine illustration of the topographical relations of the abdominal viscera; and anatomical details have been given by a large number of authors, whose works have been collected and grouped by Keith (29). So no very full account is given below.

The Stomach.

The *œsophagus* passes through the diaphragm at the level of the ninth dorsal vertebra, and opens into the stomach after an intra-abdominal course of half an inch. The stomach is divided into fundus, body, antrum, and pylorus. The fundus is well marked and projects up into the left cupola of the diaphragm. The long axis of the stomach is crescentic, and is more horizontal

than in Man. The great curvature reaches a point half an inch below the fourth lumbar vertebra, and the lowest point of the lesser curvature is level with the first lumbar vertebra. Consequently the stomach is U-shaped, and the pylorus is not far from the œsophagus. The pyloric antrum is one and a half inches long, and the pylorus, whose walls are thick, is of the same length. Between the antrum and pylorus there is a slight incisura, and there is a sudden transition from the pylorus to the duodenum. The pylorus does not project like a knob into the duodenum as it does in Man.

The *serous coat* is a uniform covering, united in the usual manner to the omenta. The *muscles* are thin, but three kinds are present. The external longitudinal layer is a complete covering, but it is thicker along the curvatures than on the intermediate parts of the body. The circular fibres are thickest; they are found in the body and pylorus, but only a few run from the œsophagus into the fundus. The oblique fibres are restricted to the fundus and part of the body to the left side of a downward prolongation of the long axis of the œsophagus, and they form rings as in Man. Consequently there are only two muscular layers—an outer one of longitudinal fibres, and an inner one of oblique fibres to the left and circular ones to the right. The *subserous and submucous coats* are thin. The *mucous membrane* is thin, and some of the gastric arteries are seen ramifying in the wall of the stomach. So thin is it that the red injection matter in the vessels shines up prominently against the pale mucosa. It is succulent and its surface shows the areas and glandular orifices as in Man. Only a few longitudinal rugæ are present.

Blood Supply:—The *coronary artery* (text-fig. 40 A) runs along the lesser curvature along with branches of the left *vagus* nerve; it gives off tortuous gastric arteries to both surfaces (*a.g.a* and *p.g.a*), and œsophageal arteries which pass up through the œsophageal opening in the diaphragm. The parent artery anastomoses with the right gastric branch of the hepatic artery. The *splenic artery* sends branches to the greater curvature (*g.c.b*) and the left gastro-epiploic artery, which anastomoses in the great omentum with the right vessel from the hepatic artery. The *hepatic artery*, in addition to the branches, sends superior pyloro-duodenal arteries downwards, and these meet with inferior pyloro-duodenal branches of the celiac axis; from both the stomach receives branches. The gastric veins open into the portal system (text-fig. 43). Barkow (2) has given an illustration of the stomach and its vessels.

Nerves:—The left *vagus* sends branches along the lesser curvature as far as the pylorus, and some other twigs form a plexus over the lower end of the œsophagus. The right *vagus* sends a rich supply of nerves to the stomach through the splenic plexus and coronary plexus, and directly.

Intestinal Tract.

The *duodenum* begins opposite the first lumbar vertebra, and it is throughout entirely behind the peritoneum. It is divided as in Man into horizontal, descending and ascending parts which measure $1\frac{1}{2}$, 2, and $2\frac{1}{2}$ inches long respectively. There is a well-marked duodeno-jejunal flexure at the level of the first lumbar vertebra. The common bile-duct and pancreatic ducts have a common opening in the descending part, but there is no papilla. No valvulae conniventes are present, and the villi are small.

The *ileum and jejunum* are 11 feet 5 inches long. Their villi are small. At intervals there are groups of small longitudinal folds of the mucosa. Four Peyer's patches are present at wide intervals in the lower half of the ileum; the lowest, which is also the largest, is 2 inches long and $\frac{3}{4}$ inch broad.

The *vermiform appendix* is $4\frac{1}{2}$ inches long, and the *cæcum* is 3 inches. No appendix valve is present, but the ileo-cæcal orifice is guarded by a shelf valve.

The *colon* is 4 feet long. It is sacculated as usual by two longitudinal muscle bands, and there are many appendices epiploicæ. No Peyer's patches are present. The most capacious part is the sigmoid colon.

The *rectum* and anal canal are $5\frac{1}{2}$ inches long. In the rectum there are eight circular folds, of which the fifth is very prominent, and below it there is a deep pocket on the left side. The anal canal shows numerous strongly-developed vertical folds of mucosa, representing the columns of Morgagni, but there are no traces of the valves of Ball. The entire rectum and anal canal form a straight tube without any trace of the flexures present in Man. Herrmann (74) has described the anal mucosa in detail.

The Peritoneum.

The *great omentum* is heavily laden with fat and reaches the symphysis pubis. All four layers are fused and can only be separated at the stomach and transverse colon. The anterior layers are attached to the greater gastric curvature, the first part of the duodenum and spleen, and bands connect it to the lateral abdominal parietes. Between the layers are the usual vessels and lymphatic glands.

The *lesser omentum* is attached as in Man, and the foramen of Winslow is large. It is bulged forwards above the stomach. Between its layers are numerous vessels, sympathetic nerves and lymphatic glands.

No gastro-pancreatic folds are present. The gastro-phrenic, gastro-splenic and lieno-renal ligaments are well-marked. A peritoneal ligament connects the lower pole of the spleen to the transverse colon, and a small accessory spleen is connected to the colon at the same point. A well-marked ligament connects the pylorus to the right ribs, but no suspensory duodenal muscle exists.

The root of the mesentery of the small intestine runs from the left side of the body of the first lumbar vertebra to the right iliac fossa. In the large intestine there is no mesentery to the cæcum, ascending, descending and pelvic colons. The appendix has a mesentery, but no other part has such a long mesentery as the iliac colon. In the rectum the peritoneum is disposed as in Man, being first surrounded by it, and then the peritoneum gradually leaves it till the lower part and the anal canal are quite devoid of a serous investment.

The Salivary Glands.

Many *labial salivary glands* are present.

The *parotid gland* (text-fig. 26) is pyramidal in shape, with the base upwards, immediately below the concha auris. The apex curves round the angle of the mandible and touches the submaxillary gland. The upper part is composed of small lobules, but the lower part is coarse. The capsule is well marked, but no lymphatic glands are included within it. Stensen's duct emerges from the upper part of the gland and its course and relations are as in Man. The relations of the gland to the large vessels and nerves are also as in Man.

The *submaxillary gland* (text-figs. 30 & 31) is flat and triangular and measures one and a half inches in diameter. It is partly under the horizontal ramus of the mandible and partly on the interramal muscles. No strong capsule exists. It is composed of superficial and deep parts, each of which is coarsely lobulated. The duct emerges from the deep surface, runs as in Man, and opens on a frenal lamella beneath the tongue.

The *sublingual gland* (text-figs. 31 and 32) is pyramidal with the apex anterior. Its relations and the course of its duct are as in Man.

Brief accounts of the glands have been given by Tyson (50) and Gratiolet (22).

The Pancreas.

Bischoff (60), Cavanna (61), Flower (20), Gratiolet (22), and Tyson (50) have given details of the pancreas. In my specimen it is flat, thin, dark in colour and coarsely lobulated. It has the usual head, body and tail, and it crosses the first lumbar vertebra. An additional process runs up along the portal vein for a short distance; and the pancreatic arteries, which are branches of the splenic, are accompanied by sympathetic nerves. The duct unites with the common bile-duct.

The Liver.

The liver much resembles that in Man. The umbilical fissure is much bridged over, and the fissure of the vena cava is also enclosed. Indications of lateral fissures exist. Near the umbilical region of the right lobe there is a small lobule directed ventrally.

The gall-bladder is superficial and extends beyond the ventral margin of the lobe and it is flexed on itself. In occasional specimens the gall-bladder is deeply embedded in the liver substance. The Spigelian lobe is subquadrate, and the caudate lobe is a triangular cone directed to the right. In some specimens the apex of the caudate lobe reaches the right margin of the liver, but in others it does not do so. The relative sizes of the hepatic lobes may be expressed by Garrod's method thus:—

$$R2 > L > Sp = C.$$

Figures or descriptions of the livers of other specimens, which agree with the above, are given by Bischoff (60), Flower (20), Barkow (2), Gratiolet (22), Cavanna (61), Symington (48), Traill (49), Tyson (50), and Sperino (47).

The relations of the abdominal organs to the vertebræ are different from those in Man, because there are thirteen dorsal vertebræ. The first lumbar vertebra in the Chimpanzee corresponds to the second lumbar vertebra in Man.

ORGANS OF CIRCULATION.

The venous side of the circulation is larger, relatively to the arterial side, than in Man.

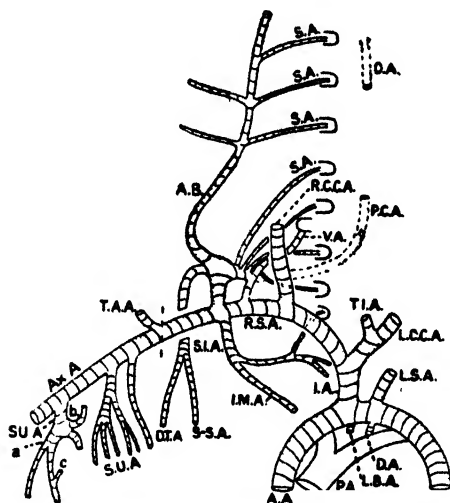
The *pericardium* adheres strongly to the central part of the diaphragm. When it is slit open the finger can explore the aortic arch up to and including the root of the innominate artery, but the reflection of the serous pericardium prevents one touching the left subclavian artery. Only a small part of the pulmonary artery is palpable.

The *heart* is small, measuring 3·2 inches long, 2·3 inches wide, and 1·7 inches antero-posteriorly. The upper border is level with the second costal cartilage, and the apex lies in the fifth intercostal space. Fat is present on the base and apex. Its internal structure is very similar to that in Man. The position and relations have been recorded or figured by Cunningham (13) and Ruge (43), and details of its construction have been given by Bischoff (60), Cavanna (61), Ehlers (59), Dwight (18), Gratiolet (22), Tyson (50), and Traill (49). The apex is entirely formed by the thick, muscular left ventricle, and this differs entirely from the condition which I have already described and figured in *Mandrillus* (62).

The pulse of a young male Chimpanzee, whose age would make it correspond to the young child, was 150 per minute. It was regular in rate and rhythm; it was full, and the rise and fall were moderately rapid. No diastole was present. The apex was not very sustained. It could easily be felt on the radial aspect of the lower end of the forearm because the radial artery is very superficial. Owing to the inability to listen to the hearts of the larger specimens in the Gardens I am unable to describe the relation between age and heart rate. The heart sounds were as in Man. The blood pressure was not obtainable.

The *aortic arch* (text-fig. 38, A.A) describes a small curve and gives way to the descending aorta at the sixth dorsal vertebra. Its relations are as in Man. It gives off the innominate and left subclavian arteries from its convexity, and the main bronchial artery to the left lung (L.B.A) arises from its concavity. The *innominate artery* (I.A), a large vessel about 2 cm. long, gives off the *left common carotid* (L.C.C.A) and divides behind the right half of the manubrium sterni into the *right common carotid* (R.C.C.A) and *right subclavian* (R.S.A) arteries. The left common carotid gives off the *thyroidea ima* (T.I.A) close to its origin. The intrathoracic parts of the left common carotid and *left subclavian* arteries are mostly as in Man, but the latter is relatively larger and not so vertical.

Text-figure 38.



The main arteries of the thorax and pectoral extremity. Ax.A: axillary artery; O.A: occipital artery; S.U.A: subscapular arteries. (Other letters in text.)

The *pulmonary artery* (text-fig. 38, P.A) is much more capacious than in Man, and its left branch is united to the aortic arch by a wide, open, ductus arteriosus (D.A). The presence of the latter, and the origin of the left bronchial artery are of interest from the embryological point of view, but the foramen ovale is closed and the venæ cavae are normal.

The ductus arteriosus is the sixth embryonic arterial arch, and the bronchial artery coming from the concavity of the aortic arch possibly represents the remains of one of the vessels connecting the outer extremities of the embryonic arches. So we have in this animal a combination of interesting embryological conditions persisting.

As the pulmonary artery is much wider than that in Man, the velocity and pressure of the blood in it must be relatively less than in him, as can be shown by applying the laws of velocity and pressure.

The *descending thoracic aorta* extends from the sixth to eleventh dorsal vertebræ after which it passes into the abdomen. It gives off the intercostal arteries to the lower ten intercostal spaces, a small bronchial artery to the left lung, a large bronchial artery to the right lung, and several branches to the thoracic œsophagus, which anastomose with œsophageal branches of the celiac axis. The lower intercostal arteries supply the diaphragm.

The *abdominal aorta* extends from the twelfth dorsal vertebra to the lower border of the fourth lumbar vertebra, where it divides into the two common iliac arteries. It is relatively smaller, and its branches are fewer than in Man. The following is the order of the branches from above downwards:—

1. Phrenic artery.
2. Celiac axis.
3. Superior mesenteric artery.
4. Renal arteries.
5. Right ovarian artery.
6. Inferior mesenteric artery.
7. Four lumbar arteries arising at different levels from the back of the aorta.

It does not give off any suprarenal arteries, nor is it continued as a middle sacral artery.

The *phrenic artery* is a large vessel arising from the left side of the beginning of the abdominal aorta. It gives a small branch to the left crus and left half of the diaphragm, and it is continued over the right crus as a large vessel which sends branches to the central tendon, the muscle fibres, the right crus, the process arising from the second lumbar transverse process and the right suprarenal capsule.

Blood Supply to the Suprarenal Capsules:—Each capsule receives a vessel from the phrenic artery and the corresponding renal artery, but none from the aorta.

The *Celiac Axis* (text-fig. 40, C.Ax) arises immediately above the upper border of the pancreas, and it quickly divides into hepatic, coronary, splenic, and inferior pyloro-duodenal arteries. Of these the hepatic is by far the largest.

The *Hepatic Artery* (H.A) first runs to the right and then turns upwards to the liver. Between the layers of the gastro-hepatic omentum it divides into two branches; and it lies in front of the portal vein, and to the left side of the common bile-duct. One of the two terminal branches (*a*) runs straight to the liver and divides into two arteries which enter the portal fissure. The other branch (*b*) runs in a convoluted course to the right, gives off the cystic artery (*c.a*) to the gall-bladder and divides into two arteries which sink into the right and left lobes of the liver.

The artery gives off a trunk which divides into:—

1. *Right gastric artery* (*r.g.a.*), which anastomoses with the left gastric artery on the lesser gastric curvature.
2. *Pyloro-duodenal vessels* (*p.d.v.*), which anastomose with the inferior pyloro-duodenal artery.
3. *Right gastro-epiploic artery* (*r.g.e.a.*), which anastomoses with branches of the splenic artery in the great omentum.

The *Coronary Artery* (C.A) is continued through the œsophagus as the œsophageal artery (*o.a.*). Branches arising from its lateral side are:—

1. *Anterior gastric arteries* (*a.g.a.*) to the anterior wall of the stomach in the fundus and body.
2. *Posterior gastric arteries* (*p.g.a.*) to the posterior wall of the stomach in the fundus and body.
3. *Left gastric artery* (*l.g.a.*), in the lesser omentum, anastomoses with the right gastric artery.

The *Inferior Pyloro-duodenal Artery* (I.P.D.A) anastomoses with branches of the hepatic and superior mesenteric arteries.

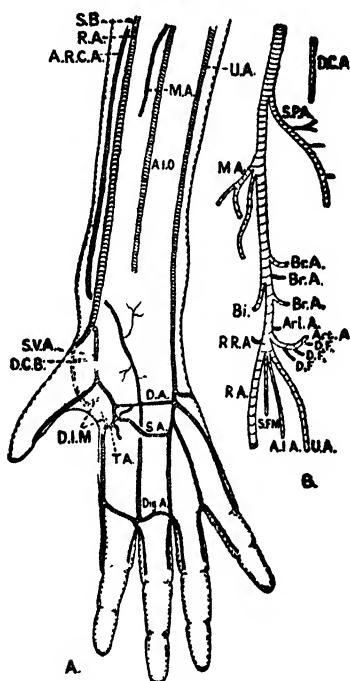
The *Splenic Artery* (S.A) runs infero-laterally and divides into two terminal splenic vessels. It gives off branches to the stomach (*g.b.*) and several vessels which form the left gastro-epiploic artery (*l.g.e.a.*) which anastomoses with the right artery. It is much smaller than the hepatic artery.

The *Superior Mesenteric Artery* (text-fig. 40 B) sweeps downwards into the right iliac fossa. It supplies the duodenum, jejunum, ileum, and large intestine as far as the right third of the transverse colon. It divides into two main branches. The trunk of the artery and left branch (*l.b.*) supply the small intestine from the duodenum to the junction of the middle and lower thirds of the ileum, the vessels for these parts coming off close together. The highest branch anastomoses with the inferior pancreatico-duodenal branch of the cœliac axis, and the lowest one anastomoses with the highest branch of the other half of the superior mesenteric artery. The trunk of the artery gives off a branch (*b.*) which bifurcates; the one half anastomoses with the lower branch of the parent stem, and its other half anastomoses in the transverse meso-colon with the middle colic branch of the inferior mesenteric artery. The arterial arcades in the mesentery are not numerous. Many glands and sympathetic nerves are mixed with the vessels.

The *Inferior Mesenteric Artery* (text-fig. 40 C) arises from the front of the abdominal aorta about three-quarters of an inch above its bifurcation. It runs downwards for half an inch and divides into two vessels which subdivide into large bundles of vessels for the iliac and pelvic colons. These vessels anastomose with one another. The parent artery gives off a large vessel, which divides into middle and left colic arteries, and the latter divides into ascending and descending branches. The *mid colic*

artery (M.C.A) supplies the left part of the transverse colon and the hepatic flexure. It anastomoses with the right colic branch of the superior mesenteric artery, and the ascending branch of the left colic artery. The *left colic artery* (L.C.A), supplying the descending colon, anastomoses with the mid colic artery and branches to the iliac colon. The *superior hæmorrhoidal artery* (S.H.A), from the right division of the parent artery, goes down to the pelvis to supply the rectum and anus. It is relatively

Text-figure 39.



The arterial supply to the pectoral extremity. A: arteries of the forearm and hand; B: arteries of the arm; A.I.O and A.I.A: anterior interosseous artery; D.C: descending branch of the circumflex arteries; M.A: median artery. Other letters in text.

larger than in Man, and replaces branches of the hypogastric artery. It divides into two terminal branches; the anterior supplies the rectum and anus, and the posterior one is limited to the rectum.

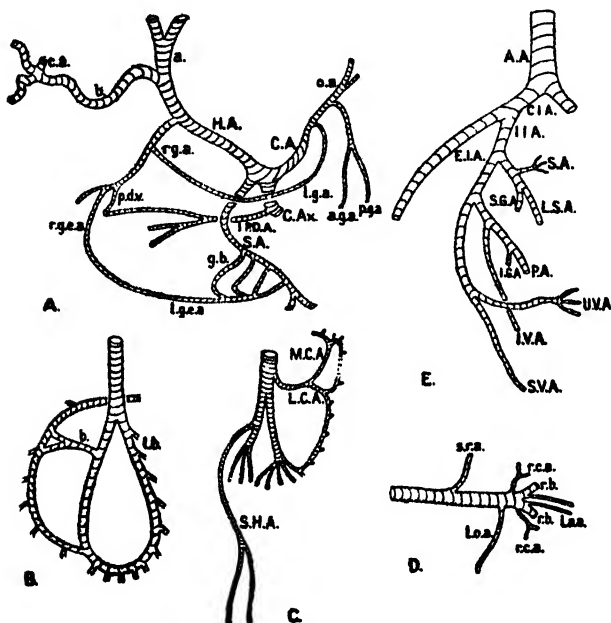
Renal Arteries:—The left vessel (text-fig. 40 D) gives off supra-renal arteries (*s.r.a.*), branches to the renal capsule (*r.c.a.*), two small arteries which anastomose with the lumbar arteries (*l.a.a.*) and the left ovarian artery (*l.o.a.*). It ends by dividing into two

vessels to the kidney. The right renal artery gives off renal, suprarenal and capsular vessels, but no parietal nor ovarian arteries.

Ovarian Arteries:—The left one comes from the left renal artery, but the right one springs from the aorta. Both run as in Man, and their terminal parts are convoluted.

Lumbar Arteries:—Four single arteries arise from the back of the aorta. The highest is level with the coeliac axis, the second is just below the renal arteries, the third is level with the third

Text-figure 40.



Arteries of the abdomen and pelvis. A: coeliac axis; B: superior mesenteric artery; C: inferior mesenteric artery; D: left renal artery; E: iliac arteries; C.I.A.: common iliac artery; E.I.A.: external iliac artery; I.I.A.: internal iliac or hypogastric artery; r.b.: arterial branches to the kidneys. Other letters in text.

lumbar vertebra, and the fourth is at the fourth vertebra. These bifurcate, and the halves run like the lumbar arteries in Man.

The *common iliac arteries* diverge for one and a half inches from the aorta, along the pelvic brim, and each gives off the hypogastric artery and is continued as the external iliac artery. The left vessel is the more vertical.

The *external iliac arteries* give no branches, but those which

arise from them in Man are here replaced by branches of the last lumbar and femoral arteries. The relations are as in Man.

The *hypogastric artery* (text-fig. 40 E) on each side divides as in Man into anterior and posterior divisions. The anterior division gives off:—

1. A trunk which divides into superior vesical (S.V.A) and uteri-vaginal (U-V.A) arteries. The former is a small vessel, which reaches the side of the bladder up which it runs to the fundus. The latter is larger and breaks up into vessels supplying the uterus and vagina; details are given on p. 401.

2. The *Pudendal Artery* (P.A) gives off the inferior vesical artery (I.V.A), passes through the great sciatic notch at the lower border of the pyriformis and, after giving off the inferior gluteal artery (I.G.A), it breaks up into branches which pass through the ischio-rectal fossa to the rectum and anus, the vagina, the levator ani and sphincter vaginæ.

The posterior division gives off:—

1. A bundle of arteries which enter the anterior sacral foramina (S.A.).

2. Lateral sacral artery (L.S.A).

3. Superior gluteal artery (S.G.A).

The *superior gluteal artery* emerges at the upper border of the pyriformis and supplies it. It divides into two main branches. The upper one supplies the gluteus medius and gives the nutrient artery to the ilium. The lower one descends to supply the gluteus medius, gluteus minimus, and scanorius.

The *inferior gluteal artery* emerges with the pudendal artery at the lower border of the pyriformis. It gives branches to the gluteus maximus, gemellus superior, obturator internus, scanorius, and acetabular part of the ilium. It anastomoses with the lateral circumflex artery.

Arteries of the Head and Neck.

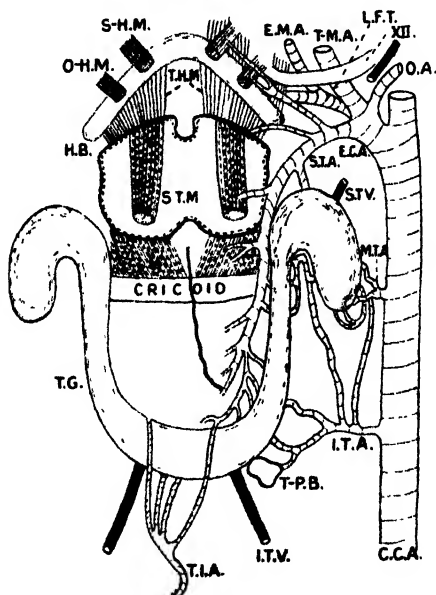
The *common carotid arteries* (text-fig. 41, C.C.A) extend from the sterno-clavicular articulations to the upper border of the lateral aspects of the thyroid cartilage, where they divide into external and internal carotids. They are concealed by the large external jugular veins, and they line in front of the vagus and sympathetic nerves. But no internal jugular veins are present to form lateral relations. No carotid sheath exists. The other relations are as in Man. It gives off tortuous inferior and middle thyroid arteries (text-fig. 41, I.T.A. and M.T.A), which replace the inferior thyroid branch of the subclavian arteries. This may be an individual peculiarity.

The *external carotid artery* (E.C.A) first ascends almost vertically till it reaches the level of the hyoid bone, where it inclines posteriorly and upwards, being continued as the temporo-maxillary artery. Within the parotid gland it divides into

internal maxillary, superficial temporal, and transverse facial arteries. The branches run in different directions. Coursing mesially are the superior thyroid (S.T.A.), a combined lingual and external maxillary trunk (L.F.T.), transverse facial and internal maxillary arteries. Running laterally is the occipital artery (O.A.), and vertically the superficial temporal, ascending pharyngeal and parotid arteries.

The *superior thyroid artery* (text-fig. 41, S.T.A.) arises almost at the beginning of the external carotid. It describes the usual

Text-figure 41.



The larynx, thyroid gland and vessels of the neck. H.B: hyoid bone; O.H.M: omo-hyoid muscle; S.H.M: sterno-hyoid muscle; S.T.M: sterno-thyroid muscle; T.G: thyroid gland; T.H.M: thyro-hyoid muscles; T.M.A: temporo-maxillary artery; T.P.B: thymus and parathyroid; XII: hypoglossal nerve. Other letters in text.

curve, with its convexity upwards, and then descends along the greater part of the mesial border of the lateral thyroid lobe. It terminates by anastomosing with the thyroidea ima (T.I.A.). It gives off mesial branches to the omo-hyoid, sterno-hyoid, sterno-thyroid, crico-thyroid and thyro-hyoid muscles; and a branch enters the larynx through the thyro-hyoid interval. The lateral branches supply the thyroid gland and anastomose with branches of the middle thyroid artery. The corresponding superior thyroid vein enters the anterior facial vein. The

combined linguo-facial artery (L.F.T) is given off at the point where the external carotid changes its direction. After an upward and forward course of half an inch it divides into lingual and external maxillary arteries.

The *lingual artery* runs horizontally and disappears under cover of the hyo-glossus muscle after giving off a large branch to the submaxillary gland. It then courses between the hyo-glossus and middle constrictor of the pharynx; and in this situation it gives off supra-hyoid and muscular arteries. Emerging from under the anterior border of the hyo-glossus, it passes forwards and dips downwards between the stylo-glossus and sublingual gland laterally and the genio-glossus mesially. It sinks into the latter, and can be traced to a communication with its neighbour below the apex of the tongue.

The *external maxillary artery* (text-fig. 41, E.M.A) runs first forwards and upwards on the upper surface of the submaxillary gland, then between the gland and the mandible. At the anterior border of the masseter it crosses on to the outer surface of the mandible and gets into the face (text-fig. 26). There it runs in a curved, but not convoluted, course to the angle of the mouth, where it becomes more vertical; and it ends in the levator anguli oris. It is concealed by the platysma and zygomatic mass, and it lies on the surface of quadratus labii superioris and buccinator. It gives off several branches to the outer surface of the submaxillary gland (S.M.G). In the face (text-fig. 26) it gives off masseteric (M.A.S), inferior labial (I.L.A), inferior coronary (I.C.A), and superior labial (S.L.A) vessels, whose distributions are shown in the figure. The submaxillary branches send vessels to the mylohyoid.

The *transverse facial artery* (text-fig. 28) runs forwards between the parotid and masseter, supplying both, and then along the zygoma.

The *internal maxillary artery* (text-fig. 29 A) has the same course as in Man, but it lies on the surface of the external pterygoid. It gives off the following branches:—

A. In the Pterygoid Region:—

1. Numerous pterygoid branches to the muscles, especially to the insertion of the external pterygoid.
2. Inferior dental artery (I.D.A) which runs as in Man along with the inferior dental nerve.
3. Meningeal artery (M.A) which passes deep to the external pterygoid, and divides into middle and accessory arteries, which enter the skull as in Man.
4. Buccal artery (B.A) accompanying the long buccal nerve.
5. Fine arteries to the suctorial pad of fat (S.P.F).
6. Posterior superior dental (P.S.D) to the gums round the molar teeth.
7. Two large, deep temporal arteries (D.T.A) which run up in the substance of the temporal muscle and anastomose freely.

B. In the Pterygo-maxillary Region:—

1. Infra-orbital artery, which passes forwards to the face. It supplies the incisor and canine teeth, some of the muscles of the face, and the upper lip.

2. Descending palatine artery to the soft palate, gums and mucous membrane of the mouth.

3. Pterygo-palatine artery to the roof of the pharynx, sphenoidal sinus, roof of the nose, and the Eustachian tube.

4. Spheno-palatine to the roof and outer wall of the nose, the ethmoidal cells, sphenoidal sinus, and pharynx.

The *Ophthalmic Artery*, which continues the internal carotid artery beyond the carotid canal is, except for its size, similar to that in Man in every way.

The *superficial temporal artery* (text-fig. 26, S.Te.A) is the apparent continuation of the external carotid artery. It runs upwards accompanied by the corresponding vein and the auriculo-temporal nerve. It divides into two branches which supply the scalp from the supra-orbital crest anteriorly to the occipital crest posteriorly.

The *transverse facial artery* (text-fig. 28, T.F.A) runs forwards between the parotid gland superficially, and the masseter deeply, supplying both by large branches. It is continued by a small artery along the surface of the zygoma.

The *occipital artery* arises from the lateral aspect of the external carotid soon after its origin. It passes upwards and backwards, and under the cleido-mastoid it gives off the *posterior auricular artery*, which supplies the parotid gland and back of the auricle. The parent stem then curves downwards and disappears under the lateral border of the splenius capitis. Under the splenius it gives off a descending branch which passes downwards among the muscles of the neck and supplies them by small twigs. The parent vessel then passes onwards under the complexus, and supplies it and the muscles bounding the sub-occipital triangle. It does not end in the scalp, nor is the terminal part crossed by the sub-occipital nerve as in Man.

The branches, with the exception of the posterior auricular artery, are distributed entirely to the muscles. No meningeal arteries run from it through the anterior condyloid foramen as in Man.

The *ascending pharyngeal artery* (text-fig. 29 B), from the back of the beginning of the external carotid runs upwards and supplies the pharynx, levator palati, tensor palati, and pre-vertebral muscles. It passes deep to the common carotid artery, and enters the jugular foramen behind the nerves. It gives off branches which form an arterial circle supplying the tonsils and pharynx.

The *internal carotid artery* is as in Man. It is accompanied by several twigs from the superior cervical sympathetic ganglion.

Arteries of the Pectoral Extremity.

Subclavian Arteries (text-fig. 38. R.S.A. and L.S.A):—The branches of the extra-thoracic parts differ from those in *Man*, but the parent vessels are similar, though relatively larger. The branches are :—

1. *Vertebral Artery* (V.A) which is very large. It enters the foramen in the sixth cervical vertebra along with sympathetic nerves from the inferior cervical ganglion of the sympathetic.

2. A large trunk whose branches correspond to separate branches of the human subclavian. Its first set of branches, which arise together, are :—

a. *Spinal Arteries* (S.A) entering the lower four intervertebral foramina behind the corresponding nerves.

b. *Profunda cervicis* (P.C.A) which passes between the transverse process of the seventh cervical vertebra and the neck of the first rib. It ascends among the muscles of the back of the neck, supplies them, and anastomoses with the occipital artery.

c. *Muscular branches to the prevertebral muscles.*

The trunk then runs outwards, gives off an *ascending branch* (A.B) to the muscles in the floor of the posterior triangle and the upper four spinal foramina and the long thoracic artery (L.T.A). Finally it divides into the *suprascapular artery* (S.S.A), and a branch corresponding to the *descending branch of the transverse cervical artery* in *Man* (D.T.A). These terminal branches course much as in *Man*.

No inferior thyroid artery is present, its place being taken by a branch of the common carotid artery.

3. *Prevertebral muscular artery.*

4. *Superior intercostal artery* (S.I.A) is large. It runs over the neck of the first rib, gives very small branches to the first two interspaces, and is continued as a very large artery into the first thoracic intervertebral foramen.

5. The *internal mammary artery* (I.M.A.) arises close to the inner border of the scalenus anticus along with the superior intercostal artery, and its relations are as in *Man*. It divides at the fifth interspace into superior epigastric and musculo-phrenic. It gives off an artery which breaks up into branches to the thymus, pericardium, and mediastinum, and anastomoses with the thyroidea ima. Muscular branches run to the triangularis sterni. But the intercostal arteries are not as regularly disposed as in *Man*. The *phrenic artery* divides into two at the seventh chondro-costal junction; one branch turns inwards and enters the diaphragmatic musculature, and the other continues along the origin of the diaphragm to the mid-axillary line where it enters the diaphragm. It anastomoses with phrenic branches of the lower intercostal arteries.

Branches of the suprascapular and descending branch of the transverse cervical arteries take the place of the superior thoracic

branch of the axillary artery in Man. No branches come from the second and third parts of the subclavian.

The *Axillary Artery* has the same course and relations as in Man. It has the additional deep relation to the axillary prolongation of the air sac. It gives off the following branches:—

1. *Thoracico-acromial axis* (T.A.A), which is not so complex as in Man. It supplies the pectoralis major, deltoid, and the fat and lymph glands in the axilla.

2. A *muscular artery* supplying twigs to the subscapularis.

3. The *subscapular artery* (S.U.A) gives off branches which arise separately in Man. These are:—*a.* A branch which runs to the inferior angle of the scapula between the teres major and latissimus dorsi, and supplies the latter; *b.* A humeral trunk, which divides into the anterior and posterior circumflex arteries. These form an anastomosis round the neck of the humerus, and the posterior circumflex gives a descending branch, which anastomoses with the profunda branch of the brachial artery; *c.* artery to the teres major; the main stem then runs down the axillary border of the subscapularis, and ends in the infraspinatus at the inferior angle of the scapula. Its circumflex branch supplies the infraspinatus, passes through the great scapular notch, and ends in the supraspinatus. There is no marked anastomosis round the scapula as there is in Man.

The *Brachial Artery* (text-fig. 39 B) differs from that in Man. It becomes the ulnar artery three inches below the internal humeral condyle. It lies superficial to the median nerve throughout, as in the Cercopithecidae. Its branches are:—

1. *Superior Profunda* (S.P.A) divides into two branches, which embrace the musculo-spiral nerve. One branch follows the nerve, anastomoses with the descending branch of the posterior circumflex artery, supplies the triceps and ends in it. An ascending twig ends in the latissimus dorsi. The other branch curves mesially round the humerus, and supplies the deltoid and triceps.

2. A large artery (M.A) to the biceps, brachialis anticus, and triceps.

3. Three muscular arteries to the brachialis anticus (Br.A).

4. Two muscular arteries to the biceps (Bi).

5. *Articular* to the elbow joint (Art.A).

6. *Radial artery* (R.A).

7. A muscular artery to the triceps and muscles arising from the external supracondylar ridge and external epicondyle (Arl.A).

8. *Articular artery* to the elbow joint.

9. Muscular arteries to the deep flexors and extensors (D.F).

10. *Radial recurrent artery* (R.R.A).

11. Muscular to the superficial flexor muscles (S.F.M).

12. *Anterior interosseous artery* (A.I.A).

There is no anastomosis round the elbow joint as there is in Man.

The *Radial Artery* (text-fig. 39 A), which is the largest vessel in the forearm, runs down the forearm very superficially, curves round the back of the wrist and over the trapezium, and passes into the first interosseous space, so it is divisible into three parts as in Man. The first part, lying in the forearm, gives off the following branches:—1. A large muscular artery to the supinator brevis (S.B); 2. Numerous fine twigs to the superficial flexor muscles; 3. *Anterior radial carpal artery* (A.R.C.A), which arises in the upper third of the forearm, runs down parallel to the radial artery, and crosses behind it in the lower part of the forearm. It ends by a series of arteries over the palmar ligaments of the inferior radio-ulnar, radio-carpal, inter-carpal, and carpo-metacarpal joints. It also supplies the flexor muscles; 4. *Superficialis volæ* (S.V.A) runs downwards and inwards across the thenar eminence and supplies its muscles. And it is continued along the inner border of the pollex. It gives off a fine twig which curves inwards and helps to form the irregular superficial palmar arch. The second part of the artery, lying on the trapezium, gives off twigs to the dorsal aspect of the inter-carpal joints (D.C.B), and a muscular artery to the first dorsal interosseous muscle (D.I.M). From the dorsal carpal branch there rises a vessel to the adjacent sides of the dorsal aspect of the index and medius. The third part of the artery lies in the interval between the palmar aspects of the index and pollex. It gives off a thenar artery (T.A) to the thenar muscles, a muscular artery to the first dorsal interosseous muscle (D.I.M), several adductor twigs and branches to the lumbricales. Over the heads of the metacarpal bones it gives a branch to the radial side of the index finger.

The *Ulnar Artery* (text-fig. 39 B, U.A) runs downwards as in Man, curves round the mesial aspect of the pisiform bone and enters the palm. It bifurcates about the middle of the palm. One branch runs to the inner border of the minimus; and the second divides into two branches which supply respectively, the adjacent sides of the minimus and annularis, and annularis and medius. From the latter branch, two arteries pass to join with branches of the radial artery and form the superficial and deep palmar arches. As the artery turns round the pisiform it gives off a dorsal branch which curves round the ulnar border of the manus to supply the tissues on the back of the ulnar border of the carpus.

The *anterior interosseous artery* (text-fig. 39 B, A.I.A) is as in Man.

Three *palmar arterial arches* are present (text-fig. 39 A):—(1) The deep arch (D.A), lying in front of the carpus, is formed by a branch of the ulnar artery, the superficialis volæ, and the branch of the radial artery to the thenar eminence; (2) the superficial arch (S.A), lying in the front of the deep arch, is

formed by the superficialis volæ and a branch of the ulnar artery; (3) a digital arch (Dig.A) over the metacarpo-phalangeal joints of the index and medius is formed by a branch of the ulnar artery with the continuation of the radial artery. The deep and digital arches are connected by a thick vessel.

The wrist joint is supplied by dorsal branches of the radial and ulnar arteries, the anterior radial carpal artery, the anterior interosseous artery, and the deep palmar arch. There is no anastomosis round the elbow joint.

The arrangements of the arteries in the pectoral extremity favour a relatively slower circulation than in Man. The profunda arteries break up into a much larger number of branches, and the brachial artery terminates in a large number of vessels which run distally in long, parallel trunks. Consequently the frictional resistance resulting from more numerous branches, combined with the relatively smaller and more uniform brachial artery slow the circulation much more. The addition of a third, or digital, arterial arch is an additional factor. As there are no anastomoses round the joints and scapula, the connections must be more numerous in the muscles, which will consequently play an important part in maintaining the circulation. And finally, the vascular arrangements are such that the head, neck, and arm get a relatively greater supply of blood than do the thorax, abdomen, and legs.

Arteries of the Pelvic Extremity.

The *femoral artery* begins about the middle of Poupart's ligament and courses downwards for an inch and a half. Then it gives off the profunda and is continued as the superficial femoral artery. The latter passes between the two parts of the adductor magnus and becomes the popliteal artery. There is no adductor canal. The common femoral artery gives off a trunk which divides into an abdominal artery and the mesial circumflex artery; and the former, after giving a nutrient artery to the ilium and the deep epigastric, is continued as the obturator artery. From the common femoral artery the deep circumflex iliac artery also arises. The profunda gives off the lateral femoral circumflex artery, and the superficial femoral artery gives off the saphenous artery, which goes down to the foot.

The *deep epigastric artery* runs up in the sheath of the rectus, but does not anastomose with a superficial epigastric branch of the internal mammary artery.

The *obturator artery* passes through the obturator foramen after running down over the horizontal ramus and back of the pubis. It supplies the symphysis pubis and muscles attached to the bone around the foramen.

The *mesial femoral circumflex artery* runs down over the head of the femur under the adductor muscles, and supplies the capsule of the hip joint, psoas, obturator internus, and adductor

magnus. It then passes round to the back of the leg and gives branches to the adductor magnus, quadratus femoris, biceps, and gluteus maximus: it also gives off the *arteria comes nervi ischiadici*.

The *deep circumflex iliac artery* runs up to the ilium. It supplies the sartorius and ilio-psoas, and ends between the internal oblique and transversalis abdominis.

The *profunda femoris* gives off the lateral circumflex and a branch passing back under the rectus femoris to the gluteus medius. It then passes through the middle head of the adductor magnus, supplies the adductor longus and vasti, and ends in the biceps. There is no series of perforating arteries as in Man.

The *lateral femoral circumflex artery* gives off:—1. an ascending branch to the glutei, rectus femoris, and hip joint; 2. a transverse artery to the gluteus maximus, vastus externus, and hip joint; 3. a descending artery to the rectus femoris, vastus externus, crureus, and hip joint.

The *popliteal artery* gives off muscular twigs to the heads of the gastrocnemius, an articular artery to the knee and a genicular trunk, the latter dividing into three branches:—1. a lateral geniculate artery which gives a nutrient artery to the femur, a branch to the back of the joint and one which passes round to the front of the capsule; 2. a mesial genicular artery which supplies the capsule in the popliteal space; 3. a descending artery which supplies the popliteus and passes through between the tibia and fibula to the anterior tibial muscles.

The *posterior tibial artery* continues the popliteal. It gives off a recurrent branch which anastomoses with the geniculars. A long branch, corresponding to the human anterior tibial artery, descends to the lower end of the posterior tibial region and curves forwards to the anterior tibial region; it gives off the following branches:—1. an artery which anastomoses with the saphenous artery and helps to form the arterial arcade on the dorsum of the foot; 2. muscular arteries; 3. malleolar arteries; 4. nutrient artery to the fibula; 5. articular arteries to the ankle. The arterial arch on the dorsum gives digital arteries to all toes except the hallux. The saphenous artery, after forming the arterial arcade, supplies the tarsal joints and gives an artery which replaces the *dorsalis pedis* in Man. This dips in between the hallux and first toe and gives a branch to the lateral side of the hallux and several muscular arteries. It then passes between the heads of the adductor hallucis and anastomoses with the deep branch of the lateral plantar artery to form the plantar arch. The latter vessel is the terminal branch of the posterior tibial artery.

The posterior tibial artery divides under the lacinate ligament into medial and lateral plantar arteries. The *lateral plantar artery* gives off the lateral calcanean artery to the skin of the heel and branches to the flexor brevis digitorum, *accessorius*, and abductor minimi digiti. It then divides into superficial

and deep divisions. The former continues as digital branches to the outer two digits; the latter passes between the heads of adductor hallucis and supplies the interossei, tarso-metatarsal joints, and anastomoses with the vessel corresponding to the *dorsalis pedis* to form the plantar arterial arch. The *medial plantar artery* gives off medial calcanean branches to the skin of the inner side of the sole of the foot and muscular branches to the abductor hallucis and flexor brevis hallucis and digital arteries to the inner three toes.

Veins of the Thorax.

Innominate Veins (text-fig. 42 B):—The left vein runs as in Man and unites with the more vertical right one to form the superior vena cava. It receives inferior thyroid (I.T.V), thymic (T.V), internal mammary (I.M.V) and superior intercostal (L.I.V) veins. The short right vein only receives the formative vessels.

The *superior vena cava* (S.V.C) is large, vertical, and enters the upper part of the right auricular appendix. It receives the vena azygos major as in Man. The thoracic part of the *inferior vena cava* is 2.6 cm. long.

The *azygos veins* drain the lower nine spaces, the first three being drained by the superior intercostal vein. All are small. No ascending lumbar veins were found. The vena azygos major enters the superior vena cava at the level of the fifth dorsal vertebra.

Veins of the Head and Neck (text-fig. 42 A).

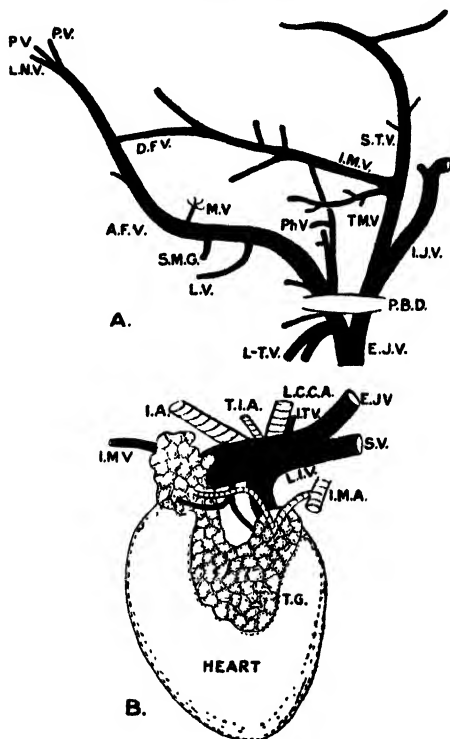
The *intra-cranial blood sinuses* have the same general arrangement as in Man. The chief difference lies in the union of the inferior petrosal and lateral sinuses within the jugular foramen to form the internal jugular vein. The groove in the skull for the right lateral sinus is much larger than that for the left, and a very shallow bony groove connects the two.

The *anterior facial vein* (A.F.V) begins by the confluence of palpebral and lateral nasal veins. It runs downwards and backwards and crosses the mandible at the anterior border of the masseter. It crosses the levator anguli oris and buccinator, and it is covered by the zygomaticus, risorius, and platysma. It runs between the mandible and sub-maxillary gland, and then under the stylo-hyoid and posterior belly of the digastric. Finally it unites with the temporo-maxillary vein to form the external jugular vein. It receives the following tributaries:—(1) *Palpebral veins* (P.V) from both eyelids. (2) *Lateral nasal veins* (L.N.V). (3) *Masseteric veins* (M.V). (4) *Deep facial vein* (D.F.V), which runs under the malar bone and buccal pad of fat to the pterygoid region. (5) *Submaxillary glandular vein* (S.M.G). (6) *Lingual vein* (L.V). (7) *Laryngeal and superior*

thyroid venous trunk (L-T.V). (8) *Pharyngeal veins* (Ph.V). No *vena transversa* exists.

The *temporo-maxillary vein* (T-M.V) is formed within the parotid gland by the union of the internal maxillary (I.M.V) and superficial temporal (S.T.V) veins. It drains the side of the head and pterygoid region and parotid gland. It receives the very short *internal jugular vein* (I.J.V), passes under the

Text-figure 42.



The cephalic veins (A) and thoracic thymus gland (B). L.I.V: superior intercostal vein ascending from behind the heart to enter the innominate vein; P.B.D: posterior belly of the digastric muscle; T.G: thymus gland (the small veins and arteries on its surface are the thymic vessels, described in the text as T.V.). Other letters in text.

posterior belly of the digastric and stylo-hyoid muscles and unites with the anterior facial vein to form the external jugular vein. The vein shows no trace of a division. No jugular bulb is present on the internal jugular vein.

It has been shown on p. 330 that there is no close pterygoid plexus, and the pharyngeal veins do not form a rich plexus.

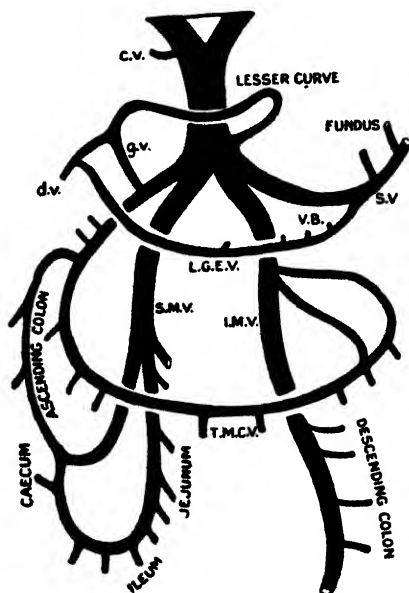
The *external jugular vein* (E.J.V) does not lie on the surface of the sterno-mastoid. It dips down and lies on the surface of the common carotid artery, vagus and sympathetic. At the outer border of the first rib it unites with the subclavian vein to form the innominate vein.

Veins of the Abdomen.

The Portal System (text-fig. 43).

The general arrangement of the tributaries of the portal system is the same as in Man, but there are differences in detail. The vein formed by the confluence of gastric, splenic and inferior mesenteric veins unites with a large trunk formed by pyloro-duodenal, superior mesenteric veins and the veins from the

Text-figure 43.



The portal vein. Letters in text.

transverse colon to form the portal vein. And the veins from the transverse colon form a connecting loop between the two systems. The portal vein begins behind the pancreas and ascends to the portal fissure in the liver behind the hepatic artery and in front of the foramen of Winslow. It divides into two large branches which enter the liver. The main vein is two and a half inches long. It is behind the pancreas, but it is later accompanied by a process of pancreatic tissue. It is surrounded and

accompanied by numerous sympathetic nerves and lymphatics. The arrangement of the system facilitates a slow and even flow of blood from the digestive organs.

Tributaries:—

1. *Splenic vein* (S.V) formed by several veins from the hilus of the spleen. It passes through the lienorenal ligament and unites behind the pancreas with the inferior mesenteric vein. It receives (a) *vasa brevia* (V.B) from the body of the stomach; (b) *left gastro-epiploic vein* (L.G.E.V) which runs along the greater curvature of the stomach, receiving veins from it, and connects the splenic and duodenal veins; (c) *pancreatic veins*.

2. *Inferior mesenteric vein* (I.M.V), which communicates with the superior mesenteric vein by a vessel which runs through the transverse mesocolon and supplies the transverse colon (T.M.C.V). It drains the large bowel from the splenic flexure to the beginning of the rectum, and it unites with the splenic vein.

3. *Superior mesenteric vein* (S.M.V), which drains the ileum and jejunum, and the large intestine from the appendix to the hepatic flexure, communicates with the venous arch in the transverse colon. At the point where it participates in the formation of the portal vein it receives the venous arch of the transverse colon, *duodenal veins* (d.v) and *gastric veins* (g.v).

4. The *cystic vein* (c.v) enters the portal trunk itself.

The Inferior Caval System.

The vena cava inferior is formed by the union of the two common iliac veins deep to the right common iliac artery. It ascends on the right side of the abdominal aorta. In the upper part of the abdomen it bends to the right and passes through a tunnel in the liver. Its relations are much as in the human body, but the right ovarian artery passes behind it. It receives:—

1. Four single *lumbar veins*, the first or lowest entering the left side of the vein, and the others pass into its dorsal surface.

2. *Right ovarian vein*.

3. Two *renal veins*.

4. *Right suprarenal vein*.

5. *Gastric vein* which serves as a link between the systemic and portal circulations.

6. *Hepatic veins*.

Veins of the Pelvic Extremity.

*Superficial Veins:—*The venous arch on the dorsum of the foot receives veins from both sides of the digits. The inner extremity is continued upwards by two internal saphena veins, which are united by cross branches. They pass upwards, dip under the sartorius and end in the femoral vein. The large external saphena vein runs up the back of the leg, dips through the fat

in the popliteal space and enters the femoral vein. There is no upward vein running through a saphenous opening, and that opening is a human characteristic.

Two *venæ comites* accompany all the branches of the posterior tibial artery. They unite to form one popliteal vein which accompanies the artery and becomes the femoral vein. The venous circulation closely follows the arterial supply, but no epigastric vein enters the femoral. The saphenous veins open, as described above, into the popliteal and femoral veins.

The *veins of the pelvis* follow the branches of the hypogastric artery, and the *hypogastric vein* joins with the external iliac vein to join the common iliac vein. The two common iliac veins unite to form the vena cava inferior. These veins have relations similar to those in Man.

Veins of the Pectoral Extremity.

The venous circulation differs in several points from that in Man. The veins of the hand unite to form the cephalic vein which only extends up as far as the antecubital fossa. There it dips inwards and unites with *venæ comites* following the branches of the brachial artery to form the brachial vein. No basilic vein is present. The brachial vein runs upwards, receiving tributaries corresponding to the branches of the artery. It is successively followed by the axillary and subclavian veins which receive tributaries corresponding to the branches of the arteries. The subclavian veins unite with the external jugular veins to form the innominate veins. The venous circulation differs from that of Man in the shortness of the cephalic vein, the absence of the basilic vein, the presence of a brachial vein instead of *venæ comites*, and the absence of an internal jugular vein uniting with the innominate vein.

THE DUCTLESS GLANDS.

The *thyroid gland* (text-fig. 41) is long, narrow, and thin. The lateral lobes are bent on themselves at the upper ends, which lie against the cricoid and lower end of the thyroid cartilage. The thicker isthmus crosses the fourth and fifth tracheal rings. There is no strong capsule and no pyramidal lobe. It receives a complicated series of arterial anastomoses from the superior (S.T.A), middle (M.T.A), and inferior (I.T.A) branches of the external and common carotids, and the thyroidea ima (T.I.A) from the left common carotid. No subclavian branches pass to the gland. The superior thyroid vein (S.T.V) opens into the anterior facial vein, and the inferior thyroid vein (I.T.V) goes to the innominate vein.

At the lower border of the isthmus there is, on each side, an oval body, the size of a pea, consisting of the *parathyroid gland* and a piece of thymus. No other parathyroid tissue was present.

The thymic constituent consisted mainly of concentric corpuscles and little lymphoid tissue. These conditions are, however, individual peculiarities.

The *thymus* (text-fig. 42), lying in the thorax, consisted of a large left part reaching the level of the third costal cartilage, and a small right part reaching the second cartilage. These parts touched over the pericardium and the left part sent a process up under the great veins. Both parts have coarse lobules, and no cavity is present in either. It is supplied by the internal mammary artery, and the veins enter the left innominate vein.

The *spleen* is small, measuring 3·8 ins. long, 2·4 ins. wide and 1·2 ins. thick. It has the same shape as in Man. The hilum is elongated. A small, oval accessory spleen is present. The artery is smaller than the hepatic artery. Other examples have larger spleens; but the form and size depend on the stages in digestion.

The *suprarenal capsules* are elongated bodies, with rounded ends, lying in the usual positions. They receive their arteries from the phrenic and renal arteries, but none from the abdominal aorta. The suprarenal plexuses are well marked.

THE BLOOD.

Gulliver (23) pointed out that the red blood corpuscles have a diameter of $1/3412$ inch, whereas those of Man are $1/3200$ inch wide. The precipitin reactions have been described by Nuttall (38) who found that the blood of the Chimpanzee gives strong, positive reactions with those of *Homo* and *Simia*, but he does not mention its reaction with those of *Gorilla* and *Hylobates*.

THE LYMPHATIC SYSTEM.

The *thoracic duct* arises from a receptaculum chyli of considerable size by two vessels, which unite later. One vessel runs upwards on the right side of the thoracic aorta, and the other courses on the posterior surface of the œsophagus. At the level of the sixth dorsal vertebra the two vessels unite to form a trunk, which runs up between the œsophagus and vertebral column, and to the left side of the former. It then passes into the neck where it opens into the junction of the left subclavian and jugular veins.

No *right lymphatic duct* was detected.

The lymphatic glands are fewer than in Man, and the following groups were isolated:—

A. *Glands in the Head and Neck*:—1. A row of small glands lying on the surface of each submaxillary gland; 2. A group of both large and small glands between the cleido-mastoid and the larynx; 3. No glands were found on the surface of the parotid or along the great vessels; 4. A group of glands over the suboccipital region.

B. Glands in the Pectoral Extremity:—1. Two small glands on the axillary surface of the *teres major* receiving vessels along the axillary vessels; 2. A row of glands, both large and small, along the course of the long thoracic artery. It is divisible into an upper group draining the glands on the *teres major*, and a lower group draining the side and back of the thoracic parietes; 3. No delto-pectoral nor cubital glands were found.

C. Thoracic Glands:—1. Several glands in the pulmonary roots; 2. Three small glands among the cardiac plexuses; 3. No retro-sternal nor vertebral glands were found.

D. Abdominal Glands:—1. Several small glands along the lesser gastric curvature; 2. Several small and large glands on the greater gastric curvature; 3. Numerous glands between the layers of the mesentery; 4. A chain of glands along the common iliac vessels.

E. Glands in the Pelvic Extremity:—1. A group of glands close to the mid point of Poupart's ligament.

It is, therefore, evident that the groups of lymphatic glands are fewer than in *Man*.

RESPIRATORY ORGANS.

The *external nose* is small, flat, and has no lateral cartilages. It is surrounded by a groove in the upper lip. Its muscles and nerves have already been described (see p. 328). The *vestibule* is well marked, and has numerous vibrissæ. The mucosa lining the nose has the orifices of numerous glands, and the upper fourths of the septum and lateral wall have striations produced by the olfactory nerves. The *septum* is as in *Man*, but I could not detect any pit corresponding to Jacobson's organ. The *inferior turbinate bone* (Pl. II. A, I.T.B) is long and almost horizontal; it is prolonged backwards by a fold of mucous membrane. The inferior meatus receives the naso-lachrymal duct (N.L.D) in its middle part. The *middle turbinate bone* (M.T.B) is bifid posteriorly, and is shorter than the lower one. On elevating it, a movable mucosa-covered bony crest is revealed, and between them lies the opening of the frontal sinus (F.S) in the middle meatus. But there is no actual bulla similar to that in *Man*. Above the middle turbinate bone there are *three turbinal crests* with four grooves. The longest is the *superior turbinate bone* (S.T.B). The *sphenoidal sinus* (S.S) is large and opens into the upper turbinal region. It is undivided and excavates the alisphenoids. The *frontal sinus* is narrow. The *antrum of Highmore* (Pl. II. B) is large, strengthened by buttresses, and has elevations produced by the roots of the canine, premolar and molar teeth. The turbinal region has been mentioned by Zuckerkandl (55), Keith (64), and Paulli (63). It has several air cells in its walls.

*Larynx**:—The *thyroid cartilage* is shaped somewhat differently from that in Man, for it has median notches both above and below. The angle between its alæ is about 90°. Its superior and inferior cornua articulate, as in Man, with the hyoid bone and cricoid cartilage. The *cricoid cartilage* is as in Man. The *arytenoid cartilage* is shaped as in Man, and the cartilages of Santorini and Wrisberg are very small. The *epiglottis* has the same shape as in Man. It is small and does not rise freely above the level of the aryteno-epiglottidean folds. The *true vocal cords* are attached to the thyroid alæ and vocal processes of the arytenoid cartilages. They are soft and flaccid, consisting almost entirely of mucous membrane, and a little elastic tissue. The *false cords* are likewise soft, and between them there are well-marked *ventricles*. The latter extend upwards behind the false cords to the aryteno-epiglottidean folds, and they are prolonged upwards by well-marked diverticula to the air-sac, which begins above at the excavated hyoid bone and extends downwards even into the axillæ. The cervical part of the pouch has already been described. This pouch is much larger than that described in many other animals, and resembles that in *Simia* in its extent. The communications between the sac and ventricles pierce the *thyro-hyoid* membrane, which is large. The *crico-thyroid membrane* is as in Man. The laryngeal joints (crico-thyroid, thyro-hyoid, crico-arytenoid) are as in Man.

Laryngeal Muscles:—The *thyro-hyoid muscle* runs from the lower half of the thyroid ala to the lower border of the hyoid bone. The *crico-thyroid muscle* runs from the anterior two-thirds of the lower border and outer surface of the cricoid cartilage to the lower border of the thyroid cartilage anterior to the inferior cornu. It is not fan-shaped as in Man. The *posterior crico-arytenoid muscle* arises from the posterior cricoid lamina, and is inserted into the processus muscularis of the arytenoid. It is more vertical and not so fan-shaped as in Man, and a small branch of the superior thyroid artery runs on its posterior surface. The *lateral crico-arytenoid muscle* runs from the upper border of the lateral part of the anterior cricoid arch to the processus muscularis. The *thyro-arytenoid muscle* does not divide as in Man. It runs from the inner surface of the thyroid ala in its lower half, near the mid plane, to the outer border of the arytenoid cartilage above the crico-arytenoid. The *oblique and transverse arytenoid muscles* are as in Man, but are diminutive, as is the ary-epiglottidean muscle.

Interior of the Larynx:—The ary-epiglottic folds are almost absent. Posteriorly the cuneiform tubercles and tubercles of Santorini are close together. The pyriform sinus is more marked than in Man. The upper division of the larynx is shallow, and the cushion of the epiglottis is well marked. The middle division is relatively larger than in Man. The false cords are 4 mm. apart. The lower part of the cavity is as in Man.

* Excellent illustrations have been published by Gratiolet (22).

The *trachea* has nineteen rings, all of which have cartilaginous hoops, with the gaps behind. The first is very wide.

Lungs:—The left lung has upper and lower lobes, and the right one has upper, middle, and lower lobes. No azygos lobe is present. The right lung receives a large bronchial artery from the descending thoracic aorta, but the left one receives a large artery from the concavity of the aortic arch, and a fine thread-like vessel from the descending aorta. Mayer (34) observed three lobes in the left lung, and two in the right. But Tyson (50), Vrolik (51), Gratiolet (22), Chapman (12), Hartmann (65), Sperino (47), and Symington (48) observed conditions similar to those in my specimen. Bischoff (60) observed two lobes in the left lung, and four in the right in an old animal. The bronchial glands are of moderate size, and adherent to the bronchi.

The limits of the *pleura* were described by Ruge (43). They presented nothing remarkable in my specimen.

UROGENITAL ORGANS (text-fig. 44).

Kidneys:—It is frequently stated that the Primates, with the exception of Man and *Ateles*, have only one renal papilla. But in this specimen, and in former animals examined by me there were respectively four and five. Ehlers (59), and Bischoff (60) noted one papilla, Symington (48) found the pyramids fused to form one papilla, and Sperino (47) noted three papillæ. The right kidney reaches lower down than the left one, and the measurements are:—

Left kidney:—5.5 cm. long; 3.3 cm. wide; 1.6 cm. thick.

Right " 6.6 " " 3.3 " " 1.8 " "

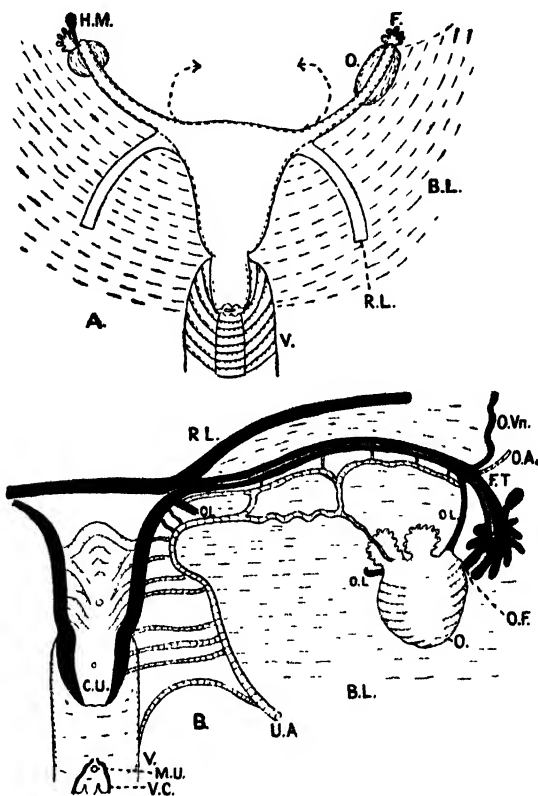
There is much peri-renal fat, but no fascial shelf supports the kidney; and there is no fat in the pelves, although Sperino (47) observed some. The capsule, which strips easily, is well vascularised. The cortex is thick, and sends prolongations in between the pyramids, which are finely striated. The blunt apices of the pyramids do not project much, and they are not embraced by large calyces. The relative positions of the structures in the hilum are as in Man, and the suprarenal capsules are similarly placed. The shape of the kidneys alters with the movements of the viscera apposed to them.

The *ureters* have the same course, relations, and terminations as in Man, but I was unable to detect lymphatics running along them between the kidneys and bladder.

The *bladder* is thick and muscular, but no urachus nor anterior ligaments are present. Lateral ligaments are well marked; and the thick round ligaments of the uterus are connected to them by peritoneal folds, so the utero-vesical pouch is crescentic. The mucosa is thick and corrugated, and the ureteric papillæ lie at the ends of prominent ridges. The patulous urethral orifice is close to the ridge, so the trigone is small. The vesical musculature consists of two layers. There is an external

longitudinal layer, half an inch wide, in the middle line. Lateral to this band the fibres run obliquely, both upwards and downwards, and interlace with one another. The submucous coat is thick, and composed of more elastic areolar tissue than in Man. The mucous membrane is loosely attached to it. The serous coat exhibits nothing peculiar.

Text-figure 44.



The internal organs of generation. A: anterior aspect; B: posterior aspect. B.L.: broad ligament; C.U.: cervix uteri; F: fimbriae; F.T.: Fallopian tube; M.U.: meatus urinarius; O.A., O.L., O.F., O.Vn.: ovarian artery, ligament, fimbria, and vein; R.L.: round ligament; V.C.: vaginal columns. Other letters in text. The arrows in figure A show the natural inward curvature of the Fallopian tubes.

Ovaries (text-fig. 44, O):—The left ovary is long, narrow and very thin, measuring $2.5 \times .5 \times .2$ cm. The right ovary is flat and rounded, measuring $1.5 \times 1.5 \times .2$ cm. Neither has any superficial scars nor rugae. Each lies vertically behind the broad

ligament at a higher level than the uterus. The histology has been described by Giacomini (66), Duval (67), and Sperino (47). Ligaments connect it to the utero-tubal junction, and to the tube below and behind the fimbriæ. The ovarian fimbria is well marked. Sperino describes triangular ovaria. The primordial ova are innumerable, and are similar to those in the human species. And Graafian follicles can be seen in various stages of development according to Sperino.

Fallopian Tubes:—Both are 6.5 cm. long when drawn straight. They hardly increase in calibre from their uterine to their ovarian ends. The fimbriæ form a dense cluster, the ovarian fimbria is well marked, and uterine and abdominal orifices are plain; but one cannot easily pass a bristle through the tube. Each tube curves over the anterior border and upper pole of the corresponding ovary. The hydatid (text-fig. 44, H.M) is well marked on the right side. The epoophoron and paroophoron are present.

Uterus (text-fig. 44):—The uterus is isolated from the bladder and rectum by peritoneal fossæ, and its summit lies 1.5 cm. above the floor of each. There is no marked fundus, the body is triangular and the cervix is fusiform. The body is 1.5 cm. long, and its base is 1.5 cm. across. The cervix is 1.2 cm. long, and 1.1 cm. across at its widest part. It has very infantile proportions. The round ligaments are large and run directly upwards and forwards from the utero-tubal junction. The interior of the body of the uterus is smooth between the tubes, but lower down it has an upward continuation of the median dorsal crest and transverse ridges which occupy the cervix. The musculature in the upper part of the uterus is thinner than in the lower part of the body and the cervix. The external os uteri is oval, with nodulated continuous lips. Both lips are of equal length. This account differs in several respects from the accounts of Sperino (47), and others. Gratiolet (22) described a bicornuate uterus.

The *vagina* is 5 cm. long, and expands from above downwards. Anterior and posterior fornices are both present, but the latter is much the larger. In its upper part there is a median dorsal cushion, and the mucosa has transverse folds. Below that it has longitudinal folds. In its lower part it has fine longitudinal striæ and several pockets (text-fig. 44). The urethra opens on its anterior wall about the middle.

The uterine artery (U.A) supplies the vagina, uterus, tubes, ovaries, epoophoron, etc. It anastomoses with the very small ovarian artery. Its complexity is shown in text-fig. 44.

The *external generative organs* (Plate I. B) are built on the same plan as, but differ from those of the human female. The *mons veneris* (M.V) is slight, and has a few hairs. The *labia majora* (L.M) are represented by slight elevations of skin over thickenings of the subcutaneous fat. The *labia minora* (L.Mi) are large and folded, and divide to surround the large clitoris (CL) the latter having two crura covered by well-developed ischio-cavernosi muscles. A small fourchette exists, but there is no

hymen. The meatus urinarius is within the vagina, so no prominent vestibule is seen as in the human condition. The glands of Bartholin lie between the vagina and rectum. Sperino (47), Bischoff (60), Chapman (12), Gratiolet (22), Hartmann (65), Barkow (2), Hoffmann (68), Symington (48), and Traill (49) have described the external genitalia; and many of these observers have described the internal organs.

Winwoode Reade (57), Garner (21), and Mohrike (35) describe a sexual season, and Bolau (5), Ehlers (59), Hermes (69), and Keith (30) describe either the periodicity or characters of menstruation. Pocock (80) contrasts menstruation in the Chimpanzee and Hainan Gibbon.

THE NERVOUS SYSTEM*.

The *olfactory nerve* terminates by marked branches on the upper thirds of the turbinate regions and nasal septum.

The *optic nerve* is large and surrounded by a sheath of dura mater. No *arteria retinæ centralis* was detected in it, but the injection material may not have traversed it.

The *oculo-motor nerve* has superior and inferior divisions. The superior division does not pierce, but runs to the inner side of, the superior rectus. It supplies the superior and internal rectus muscles and ends in the levator palpebræ superioris. The inferior division runs downwards and outwards on the outer side of the rectus inferior, gives a motor branch to the ciliary ganglion, supplies the inferior rectus and ends in the inferior oblique. The branch of the superior division to the internal rectus is very large.

The *trochlear nerve* ends by three divisions to the superior oblique muscle.

The *trigeminal nerve* has three divisions as in Man, radiating from the Gasserian ganglion. The ophthalmic division courses as in Man, and breaks up into:—1. *Lachrymal nerve*, lying between the orbital wall and upper border of the external rectus. It supplies the lachrymal gland, conjunctiva and skin of the eyelids. 2. *Frontal nerve* resembles that in Man. It breaks up into supra-orbital and supra-trochlear branches. 3. *Nasal nerve*. This is distributed as in Man, but the lateral terminal branch, which is very large, comes out of the nasal cavity direct, and not between bone and cartilage, as in Man. The *ciliary ganglion* is larger than in Man. It lies on the lateral side of the ophthalmic artery and receives filaments from both divisions of the third nerve, a twig from the naso-ciliary nerve, and sympathetic filaments from the carotid plexus. It gives off short ciliary nerves: one large one, lying on the outer side of the optic nerve, divides into upper and lower divisions on reaching the eyeball. The superior and inferior maxillary divisions of the trigeminal are similar to those in Man, but I was unable to detect as many branches radiating from Meckel's ganglion. The *chorda tympani*

* The brain will be described in a separate paper by Professor G. Elliot Smith, F.R.S.

joins the inferior maxillary division before the latter separates into its lingual and inferior dental nerves. The submaxillary ganglion is not separate as in Man, but is fused with the hypoglossal nerve. The otic ganglion was not recognised with certainty.

The *abducens* emerges between the two heads of the external rectus and sinks into the ocular surface of the muscle.

The *facial nerve* emerges from the stylo-mastoid foramen. Its intra-petrous course was not traced. It divides in the parotid gland into temporal, zygomatic, maxillary, buccal, mandibular, and cervical divisions. The temporal branches run upwards and are distributed as in Man. The zygomatic and maxillary divisions eventually unite and give off from their combined trunk a number of branches to the muscles of the face. The mandibular and cervical divisions are as in Man. The union of the chorda tympani and trigeminal nerves has already been described.

The *auditory nerve* was not traced.

The *glosso-pharyngeal nerve* emerges from the inner part of the jugular foramen and communicates with the other nerves at the upper part of the neck. It passes between the external and internal carotid arteries, curves round the stylo-pharyngeus muscle and disappears under the free outer edge of the hyoglossus. Finally it breaks up into branches to the tongue, pharynx, and tonsil. It supplies the stylo-pharyngeus. The tympanic and petrosal branches were not traced.

The *Vagus Nerve* (text-figs. 45 & 46) emerges from the jugular foramen wherein it is lateral to the glosso-pharyngeal nerve, posterior to the internal jugular vein and mesial to the accessory nerve, to which it is closely adherent. Immediately below the base of the skull it develops the ganglion nodosum (G.N.) on its lateral aspect. The nerve separates from the ganglion again at the level of the posterior border of the hard palate. At the root of the neck it runs on to the posterior aspect of the common carotid artery and then it enters the thorax on the left side. The right one disappears under cover of the innominate artery where the latter bifurcates into right common carotid and subclavian arteries. The left vagus (text-fig. 45 A) only communicates with the sympathetic, but the right one (text-fig. 45 B) is extensively used with the sympathetic.

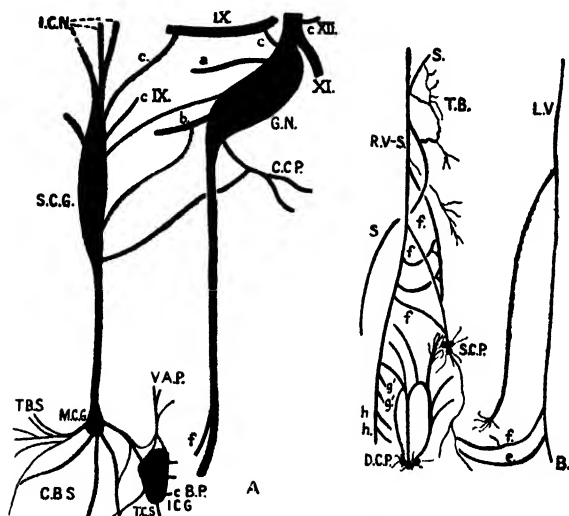
Branches in the Neck :—

1. Communicating nerves to the glosso-pharyngeal (c. ix), hypoglossal (c. xii), superior cervical ganglion of the sympathetic (S.C.G) and cervical plexus (c.C.P).
2. Pharyngeal nerve (a).
3. Superior laryngeal nerve (b).
4. Right recurrent laryngeal nerve (d).
5. Cardiac branch of the left vagus (f).
6. Plexus of carotid, tracheal and cardiac branches of the right vagus.

The *left thoracic vagus* (text-fig. 45 B) has the same relations and course till it reaches the posterior aspect of the pulmonary root as in Man. It gives off recurrent (*e*), cardiac (*f*), and anterior pulmonary nerves. Behind the root of the left lung it gives off posterior pulmonary nerves. It does not break up into the posterior pulmonary plexus as it does in Man. Leaving the back of the root of the lung it gains the front of the œsophagus, which position it maintains into the abdomen. It supplies the œsophagus and pleura and communicates with the right vagus.

The *right thoracic vagus* (text-fig. 45 B) gets into the thorax after crossing the right subclavian artery, at which point it gives off its recurrent branch. It crosses the right side of the trachea

Text-figure 45.



The vagus and sympathetic nerves. A: cervical parts of the left vagus and sympathetic; B: thoracic parts of the left vagus and the cervical and thoracic parts of the right vagus and sympathetic. Letters in text.

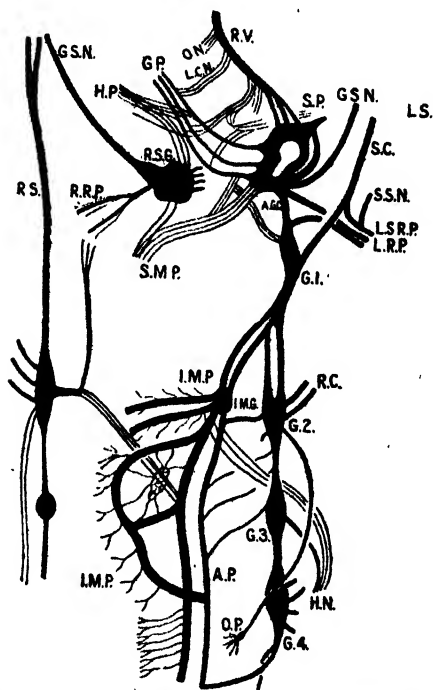
from before backwards and it is crossed by the vena azygos major. It passes down the back of the right pulmonary root and inclines downwards and backwards to reach the dorsal aspect of the œsophagus. There is no plexus gulæ. It gives off three cardiac nerves (*f*), three anterior pulmonary (*g'*), two tracheal (T.B), two posterior pulmonary (*h*), and several œsophageal nerves.

Abdominal Parts of the Vagi (text-fig. 46):—The *left vagus* passes through the anterior part of the œsophageal opening in the diaphragm, and divides into two. One branch divides into twigs which run along the lesser curvature as far as the pyloric antrum. The other branch gives twigs along the lesser curvature,

twigs running along the œsophageal branch of the celiac axis, coronary plexus, and œsophageal nerves, which ramify over the lower end of the œsophagus. It anastomoses with branches of the right vagus. The *right vagus* (R.V) passes through the posterior part of the œsophageal opening in the diaphragm, and it ends in the left semilunar ganglion. The branches are very numerous and extend widely in the abdomen. They are:—

1. *œsophageal nerves* (O.N) to the back of the lower end of the œsophagus.

Text-figure 46.



Abdominal parts of the vagus and sympathetic nerves. Letters in text.

2. *Gastric nerves* (L.C.N) running along the lesser curvature of the stomach.

3. Twigs to the hepatic (H.P), coronary (G.P), splenic (S), superior mesenteric (S.M.P), inferior mesenteric (I.M.P), and aortic (A.G.C) plexuses. The twigs can be traced far into the plexus, some in fact being so well marked that they can be followed to the organs. I did not trace twigs as far as the cæcum nor could I trace them to the sigmoid and rectum.

The *Spinal Accessory Nerve* emerges as in Man from the jugular foramen, pierces the cleido-mastoid, runs deep to the sterno-mastoid and gains the deep surface of the trapezius, where it has already been described. It supplies the cleido-mastoid, sterno-mastoid and trapezius, and it communicates with the cervical plexus, but not with the sympathetic.

The *Hypoglossal Nerve* emerges as in Man from the skull, and has a similar disposition till it reaches the hyo-glossus muscle. At the anterior border of that muscle it forms a loop and exhibits a swelling slightly anterior to it. This swelling receives filaments from the lingual nerve, and there is no separate submaxillary ganglion. Finally it divides into twigs for the stylo-glossus and genio-glossus. Branches:—(1) On the left nerve there is a strong *descendens hypoglossi*, but it is replaced by two branches on the right side. (2) Nerve to the *thyro-hyoid muscle*. (3) Nerves to *genio-hyoid*. (4) *Communicating to the lingual nerve*. (5) Nerves to *genio-glossus*. (6) Nerves to *stylo-glossus*.

The Cervical Plexus (text-fig. 47).

The cervical plexus is formed from the first four cervical nerves, and its relations are similar to those in Man; but there are differences in the branches. The first and second nerves form a loop. Branches of the second and third nerves form cords; a mesial cord forms the nerve to the sterno-hyoid (S-H.M.) and a lateral cord forms the transverse cervical (T.C.N.) and occipital nerves (O.N.). Branches of the third and fourth nerves form the descending supraclavicular nerves (S-C.N.). The fourth nerve communicates with the fifth.

Branches:—

I. *Superficial Cutaneous Nerves*:—Small occipital (O.N.) and transverse cervical (T.C.N.) from C2 and C3; Descending branches (acromial, sternal, and clavicular) from C3 and C4.

II. *Deep Muscular Branches* to sterno-mastoid (S-M. from C2), trapezius (TRA. from C3 and C4), levator anguli scapulæ (L.A.S. from C3), scalenus medius (Scal. Med. from C4), omo-hyoid (O-H.M. from C2), sterno-thyroid (S-T.M. from C2), sterno-hyoid (S-H.M. from C2 and C3), and diaphragm (by phrenic (P.N.) from C2, C3, C4, C5).

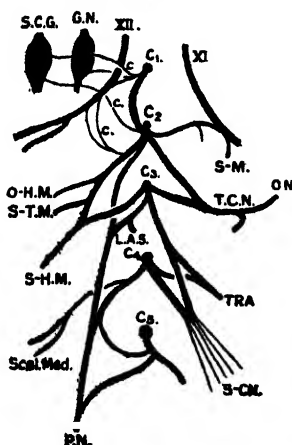
III. *Deep Communicating Branches* to vagus (G.N.), accessory (xi) and hypoglossal (xii) from C1 or C2. There are no separate branches to the sympathetic on the left side, but the ganglion nodosum and superior cervical sympathetic ganglion are connected close to the spot where the vagus communicates with the cervical plexus. On the right side communications go from the sympathetic ganglion to the first and second cervical nerves.

There is no marked *ansa hypoglossi*.

The *Phrenic Nerve* (P.N.) is mainly derived from the fourth cervical nerve, but it receives fine fibres from C3, C2, and C5.

It passes downwards through the neck on the scalenus anticus and it enters the thorax between the subclavian artery and vein. Its general relations to the aortic arch, vagus, heart, and root of the lung are the same as in Man. Close to the diaphragm it divides into five branches which subdivide. Some of these supply the thoracic surface of the muscle, but others pass through it to

Text-figure 47.



The cervical plexus. C1-C5: cervical nerves. Other letters in text.

supply the abdominal surface. It is accompanied by an artery and a vein. It gives branches to the pleura and pericardium, and communicates with the phrenic sympathetic plexus, but I did not trace branches of this anastomosis to the inferior vena cava, hepatic, and suprarenal plexuses. No arteria comes nervi phrenici was seen.

The Brachial Plexus (text-fig. 48).

The plexus is formed by the lower four cervical and first dorsal nerves as in Man, but the arrangements differ. Before they form the plexus C5, C6, and C7 give off the three roots of the *long thoracic nerve* (L.T.N), and a well-marked branch runs from the upper roots to the first digitation of the serratus magnus (Serr. Mag). C7 and C8 also give twigs to the scalenus anticus (*Scal. Ant.*).

C5 unites with the anterior division of C6 after giving off:—
1. A nerve to the levator anguli scapulae (L.A.S), the rhomboidei (R.M) and the first digitation of serratus magnus (S.A.M);
2. the *suprascapular nerve* (S-S.N). As C5 joins a division of C6 there is no upper trunk as in Man.

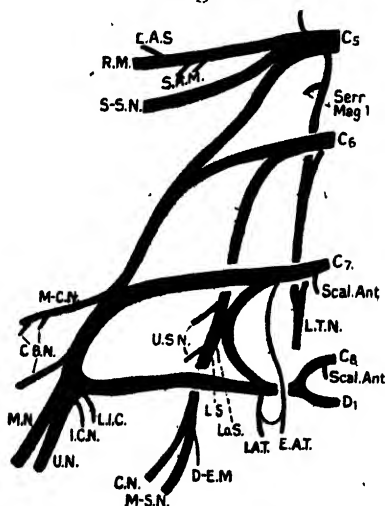
C6 divides into anterior and posterior divisions.

C7 gives off the *external anterior thoracic nerve* (E.A.T) and forms a trunk which divides into anterior and posterior divisions as in Man.

C8 and D1 unite to form a short trunk which divides into anterior and posterior divisions. At the point of division the *internal anterior thoracic nerve* (I.A.T) is given off. The two anterior thoracic nerves are connected by a loop as in Man.

C5 and the anterior divisions of C6 and C7 unite to form a thick cord which, after giving off the *musculo-cutaneous nerve* (M-C.N), unites with the anterior division of the combined C8 and D1 to form a cord, which divides into *median* (M.N) and *ulnar* (U.N) nerves. There is no separation into outer and inner cords as in Man, but the musculo-cutaneous nerve represents the former.

Text-figure 48.



The brachial plexus. C5-D1: lower cervical and first dorsal nerves.
Letters in text.

The posterior divisions of C6, C7, and the combined C8 and D1 unite to form a posterior cord, which gives off four *subscapular nerves* (U.S.N., L.S., Lo.S) and divides into the *musculo-spiral* (M-S.N) and *circumflex* (C.N) nerves.

The *internal cutaneous* (I.C.N), *lesser internal cutaneous* (L.I.C), and a *coraco-brachial* (C-B.N) twigs come from the representatives of the outer and inner cords.

The *suprascapular nerve* from C5, passes through the suprascapular notch, supplies supra-spinatus and turns through the great scapular notch to supply infra-spinatus. As it passes through the greater notch it gives a second branch to the supra-spinatus.

The *musculo-cutaneous nerve* from C 5, C 6, C 7, gives a branch to the coraco-brachialis and then pierces the muscle. It then gives a large branch to the biceps. Finally it divides into a muscular trunk to the brachialis anticus, and a cutaneous trunk, which gives a small nerve to the spinator longus.

Four *subscapular nerves* are present. The two upper ones go to the upper and lower parts of subscapularis. The long subscapular communicates with the musculo-spiral nerve and supplies the latissimus dorsi. The lowest nerve supplies the subscapularis and teres major.

The *median nerve* arises from the anterior divisions of all the nerves forming the plexus. It almost immediately after its formation gives a small branch to the coraco-brachialis. No branches arise in the arm. Just below the bend of the elbow it supplies the flexor carpi radialis, flexor sublimis, and both heads of the pronator radii teres. Then it communicates with the ulnar nerve by a thick branch. In the middle of the forearm it supplies the radial fibres of the flexor sublimis digitorum. About an inch distal to the radio-carpal joint it bifurcates. The outer division supplies the thenar muscles, first lumbrical, and the skin of the radial side of the index and ulnar side of the thumb. The inner division gives a small twig to the third and fourth lumbricals. Then it divides to supply adjacent sides of the second and third and fourth digits. The nerve to the second and third digits also supplies the second lumbrical. All the branches pass deep to the superficial palmar arch.

The *circumflex nerve* gives the nerve to the teres minor before it passes through the quadrilateral space. No definite anterior and posterior divisions are present. After giving off the large lateral cutaneous nerve of the arm it breaks up into deltoid branches.

The *ulnar nerve* arises in common with the median. Its course is much as in Man. In the forearm it supplies the flexor carpi ulnaris and flexor profundus digitorum and communicates with the median nerve. Two inches proximal to the wrist it divides into anterior and posterior divisions. The former supplies the hypothenar muscles, the skin of the adjacent sides of the annularis and minimus and the inner side of the minimus; and the latter goes deeply to supply the palmar interossei. A dorsal branch leaves the main trunk at the level of the pisiform bone and supplies interossei.

The *musculospiral nerve* from the posterior divisions of C 6, C 7, C 8, gives off a slender, but long, nerve to the dorso-epitrochlearis. Its course is as in Man. In the arm it gives off branches to the triceps and skin as in Man. In the lower part of the arm it supplies the supinator longus and extensor carpi radialis longior. At the bend of the elbow it divides into radial and posterior interosseous nerves. The former runs down to the skin of the wrist. The latter perforates the supinator brevis. It supplies the extensores carpi radialis longior and brevior, and the muscles

on the extensor aspect of the forearm. Finally it sends a long, fine nerve to the wrist joint.

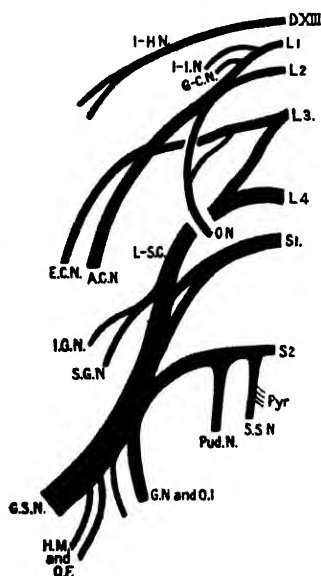
The *internal cutaneous* and *lesser internal cutaneous* nerves arise from the conjoined median and ulnar nerves in the brachial plexus. They are distributed as in Man.

The intercosto-humeral nerve is as in Man.

The Lumbar and Sacral Plexuses (text-fig. 49).

The lumbar plexus is formed by the anterior primary divisions of the four lumbar nerves, the sacral plexus is formed by the

Text-figure 49.



The lumbo-sacral plexus. DXIII-S2: nerves forming the plexus proper; S3 and S4, not shown in the diagram, supply pelvic muscles; Pyr: nerves to pyramiformis; H.M. and Q.F.: nerves to the hamstring muscles and quadratus femoris. Other letters in text.

anterior primary divisions of the four sacral nerves. The two plexuses are connected by the lumbo-sacral cord from the third and fourth lumbar nerves. Hepburn (24) gives the cord as coming from the fourth lumbar, Champneys (11) records a totally different formation of the plexuses, but does not mention the cord. Bolk (7) showed that there are slight variations in different animals.

The following table shows the origins of the nerves as observed by myself and others :—

Nerves.	BOLK.	HEPBURN.	CHAMPNEYS.	Self.
Ilio-hypogastric ...	D xiii. D xiii.	Not recorded.	D xiii.	D xiii.
Ilio-inguinal.....	D xiii. D xiii. L1	L1	D xiii.	L1
Genito-crural	L1	D xiii.	L1
Anterior crural.....	L1, 2, 3	L1, L2, L3	D xiii., L1, L2, L3	L1, L2, L3
Lateral cutaneous...	L1, 2	L2, L3	D xiii., L1	L2, L3
Obturator	L2, 3; L1, 2, 3	L2, L3, L4	D xiii., L1, L2	L1, L2, L3
Superior gluteal ...	Liv., S1	L-S.C, S1	Liii., L iv., S1	L-S.C, S1
Inferior gluteal ...	Liv., S1, S2	Small sciatic.	Not recorded.	Sup. gluteal.
Great sciatic	L-S.C, S1, S2	L-S.C, S1, S2
Small sciatic.....	Not recorded.	Liii., L iv., S1	S2
Pudendal	S2	Not recorded.	Not recorded.	S2
N. Obturator Int....	Tibial nerve.	S1, S2	Not recorded.	S2
N. Pyriformis	Peroneal nerve.	S2	S2	S2
N. Quadratus Fem.	Tibial nerve.	S1, S2	Not recorded.	Great sciatic.
N. to Gemelli	S1, S2	Not recorded.	S2

It is evident that D xiii. and L1 correspond to L1 and L2 of Man. It is also evident that the branches of the plexus are liable to considerable variation in different animals, and I found some differences on both sides in my own. For example, the obturator nerve came from L2 and L3 on the right side, but from L1, L2, L3 on the left.

The *ilio-hypogastric nerve* (I-H.N) is the continuation of D xiii., and it is distributed as in Man. The *ilio-inguinal* (I-I.N) and *genito-crural* (G-C.N) nerves are also as in Man; the former is large.

The *anterior crural nerve* (A.C.N) divides into anterior and posterior divisions in the upper part of Scarpa's triangle. The former gives off a cutaneous patellar branch, the cutaneous saphenous nerve and muscular branches to the sartorius, gracilis, and pectineus. The posterior division supplies the quadriceps extensor and the hamstring muscles*.

The *obturator nerve* (O.N) divides into inner and outer parts between the inner and outer heads of the adductor brevis. The former emerges to the outer side of the superficial head of the muscle and supplies the pectineus, gracilis, adductor longus, and adductor brevis. The latter emerges to the inner side of the superficial head and supplies the adductor magnus, adductor brevis, and obturator externus. No branch accompanies the popliteal artery.

The *lateral cutaneous nerve* (E.C.N) branches off from the anterior crural nerve, and is distributed as in Man.

The *great sciatic nerve* (G.S.N) at first supplies the obturator

* This distribution to the hamstrings was not observed in another Chimpanzee.

internus, gemelli, quadratus femoris, biceps, and gluteus maximus. As it courses round the tuber ischii and down the thigh it gives branches to the hamstrings. In the popliteal space it divides into external and internal popliteal nerves. The *external popliteal nerve* passes under the biceps and through the extensor longus digitorum and supplies both. It is continued as the *anterior tibial nerve*. The latter supplies the anterior tibial muscles at the top, the ankle joint, the flexor brevis digitorum, the tarso-metatarsal joints and the skin of the adjacent sides of the hallux and index. It gives off the *musculo-cutaneous nerve* which, however, only supplies the skin of the adjacent sides of the index, medius, annularis, and minimus. No *nervus suralis* exists. The internal popliteal nerve becomes the *posterior tibial nerve*. This passes between the heads of the gastrocnemius and supplies them. As it passes down the leg it gives a branch to the upper part of the anterior tibial muscles and branches to the posterior tibial muscles, peronei, ankle joint, and flexor brevis digitorum. It divides into three terminal branches. A muscular branch runs to the abductor minimi digiti. The internal plantar nerve, or second terminal branch supplies the abductor hallucis, lumbricales, flexor brevis hallucis, adductor hallucis, joints of the foot, and the skin of the inner four toes. The nerve to the last digit communicates with the lateral plantar nerve. The lateral plantar nerve, or third terminal branch divides into superficial and deep parts. The former supplies the abductor and flexor and skin on the outer side of the fifth toe. The latter supplies the adductor hallucis, interossei, and tarso-metatarsal joints.

The *superior gluteal nerve* (S.G.N) emerges above the pyriformis, and divides into two branches which follow those of the artery. A special branch runs to the gluteus minimus, but the scanorius is supplied by the sciatic nerve.

The *inferior gluteal nerve* (I.G.N) accompanies the corresponding artery to the gluteus maximus.

The *pudendal nerve* (Pud.N), after emerging through the sciatic notch, forms a prominent cord lying alongside the pudendal vessels. It lies in the outer wall of the ischio-rectal fossa, but no well-marked Alcock's canal exists. It gives several twigs to the rectum, external sphincter ani, levator ani, sphincter vaginae, and ischio-cavernosus. It also supplies the skin of the perineal region. It differs from that in Man in that it does not pierce any triangular ligament, and it has no branches to the transverse perineal muscles, for the latter are absent. It does not divide into two terminal branches of large size.

The *small sciatic nerve* (S.S.N) courses much as in Man.

I agree with Bolk (7) that the Chimpanzee, like the other Anthropoids, differs from Man in the absence of a *nervus suralis*.

The lumbar and sacral nerves receive grey rami communicantes from the gangliated cords of the sympathetic nerves (text-fig. 46).

The Sympathetic Nervous System (text-figs. 45 & 46).

The long, oval *superior cervical ganglion* (S.C.G) extends from the level of the hard palate to the hyoid bone. It is connected by communicating branches to the ninth (IX) and twelfth cranial nerves, and to the ganglion nodosum (G.N) and its superior laryngeal (b) branch. On the left side it sends no twigs direct to the cervical plexus, but it is connected to the first and second cervical nerves on the right (text-fig. 45 A.) It gives off pharyngeal nerves and the external carotid plexus, but no cardiac nerve arises from it. The internal carotid branch (I.C.N) breaks up into a plexus before it enters the skull.

The left sympathetic runs separate from the vagus and ends in the *middle cervical ganglion* (M.C.G) whence the following branches radiate:—(1) A stout cord which divides into branches accompanying the thyroidea ima artery to the thyroid gland (T.B.S), tracheal nerves and cardiac nerves (C.B.S) to the deep part of the cardiac plexus and plexus round branches of the aortic arch. (2) Nerves to the cardiac and aortic plexus (C.B.S) (3) Continuation of the cord to the inferior cervical ganglion (I.C.G). This also communicates with the vertebral plexus (V.A.P), brachial plexus (c.B.P), and cardiac plexus.

The right sympathetic fuses with the right vagus, but separates from it lower down again, and a rich plexus of nerves comes from it, both above and below, and accompanies the common carotid artery to the plexus on the branches of the aortic arch. The middle ganglion does not send off many radiations as on the left side.

The *inferior cervical ganglion* (I.C.G) and first thoracic ganglia are fused. It gives off rami communicantes to the brachial plexus (c.B.P), a thick plexus which accompanies the vertebral artery (V.A.P), a nerve to the cardiac plexus, and the thoracic sympathetic cord (T.C.S).

The *Thoracic Cords* have fewer ganglia than the number of intercostal nerves. The left one gives off the great splanchnic nerve (G.S.N) at the level of the fifth and sixth thoracic nerves. At the level of the diaphragm it divides into the small splanchnic nerve (S.S.N) and abdominal sympathetic cord (S.C). In addition to these it gives off rami communicantes to the intercostal nerves and some of these are long. Aortic nerves accompany the intercostal arteries to the plexus around the aorta, and some of these reach the root of the lung, but were very delicate at that region.

Abdominal Cords (text-fig. 46):—The left cord runs down and passes under the left renal artery. It possesses four ganglia. The first (G.1) lies at the level of the superior mesenteric artery. The cord which emerges from it gives off nerves to the inferior mesenteric plexus (I.M.P) and divides into two. The halves are collected again into the second ganglion (G.2); this gives off rami communicantes (R.O) to the first two lumbar nerves, a

branch to the inferior mesenteric plexus, and the ovarian plexus (O.P). The cord connecting the second and third ganglia gives twigs to the aortic plexus (A.P). The third ganglion (G.3) lies at the beginning of the common iliac artery. It gives off rami communicantes to the lower two lumbar nerves, hypogastric nerves (H.N) and the external iliac nerves. The fourth ganglion (G.4), situated within the pelvis, gives off strong rami communicantes to the sacral nerves, and a nerve to the hæmorrhoidal plexus. The right cord has two abdominal and one pelvic ganglia. The first ganglion gives rami communicantes to the lumbar nerves from its lateral aspect. From its mesial aspect a stout cord comes and divides into an upper branch to the left renal plexus (L.R.P) and a lower bunch of three nerves to the inferior mesenteric plexus (I.M.P). The second ganglion is at the level of the common iliac artery.

Vagus and Sympathetic Plexuses.

A. *Pharyngeal Plexus*:—This is formed by branches of the glossopharyngeal nerve and sympathetic, and the pharyngeal branch of the vagus.

B. *Cardiac Plexus* (text-fig. 45 B):—The cardiac plexus lies chiefly between the aortic arch and heart anteriorly, and the trachea posteriorly. It receives two cardiac branches of the left vagus. One rises in the neck and divides into four branches on the front of the aortic arch; two of the branches pass under the arch to the deep part of the plexus, the third runs to the surface of the arch, and the fourth supplies the pulmonary artery. No sympathetic filaments run over the arch to the superficial part of the plexus (S.C.P). The deep part of the plexus (D.C.P) communicates with the superficial part and receives:—(1) Many filaments from the left sympathetic, a thoracic cardiac branch of the left vagus, the cervical cardiac branch of the right vagus, three thoracic cardiac branches of the right vagus and filaments from the right cervical sympathetic. The plexus contains two clusters of ganglia, one behind the beginning of the innominate artery, and the other between the aortic arch and bifurcation of the trachea. The large vessels arising from the arch have associated plexuses or sympathetic nerve cords.

C. *Anterior pulmonary plexuses* derived from the vagi. No separate sympathetic filaments are seen.

D. *Posterior pulmonary plexuses* derived from the vagi and upper thoracic ganglia of the sympathetic.

E. *Solar Plexus* (text-fig. 46):—The gangliated ring, which acts as a centre, lies in front and at the sides of the celiac axis. It receives the greater part of the right vagus (R.V) and the great splanchnic nerve of the left side (G.S.N). It gives off a trunk at its lower end which runs into the gangliated cord of the sympathetic of the left side (A.G.O). It gives off the celiac

plexus, which breaks up into gastric (G.P), splenic (S.P), and hepatic (H.P) plexuses. It sends off the superior mesenteric (S.M.P), left renal (L.R.P) and left suprarenal (L.S.R.P) plexuses.

F. Inferior Mesenteric Plexus (I.M.P):—A well-marked ganglion (I.M.G) is present. It supplies the descending colon and rectum and communicates with the left abdominal sympathetic cord.

The right celiac ganglion (R.S.G) receives the great splanchnic nerve. It is connected to the left ganglion by several communicating nerves. Offshoots go into the celiac, right renal and superior mesenteric plexuses.

G. The right and left renal plexuses (L.R.P. and R.R.P) are offshoots of the corresponding halves of the solar plexus. They receive splanchnic nerves and branches from the abdominal sympathetic cords.

H. The ovarian plexuses (O.P) are offshoots of the abdominal sympathetic ganglia.

The Eye and its Appendages (text-fig. 27).

The skin over the supraorbital margin has a few long hairs running in different directions, but there are no pronounced eyebrows. The upper lid is longer than the lower, and has longer cilia. The Meibomian glands form projections on the back of the lid, but a strip of darkly-coloured conjunctiva prevents them from forming ridges on the ocular surface of the lid. The capacious lacus lachrymalis is lined by black conjunctiva. No caruncula is present, but the plica semilunaris is well marked. The bulbar conjunctiva is dark in colour, but only the marginal part of the palpebral conjunctiva is pigmented. The lower lachrymal papilla is larger than the upper one, and the internal tarsal ligament is larger than the lateral tarsal raphe.

The *lachrymal gland* is small and flat, and consists of two parts as in Man. The ducts open into the superior conjunctival fornix. And the naso-lachrymal duct opens below the inferior turbinate bone into the middle of the inferior nasal meatus (Pl. II. fig. A). The gland is deeply embedded in thick fat.

The fascia is very strong, and is attached as in Man to the tarsal ligaments.

Orbital Muscles:—The *levator palpebræ superioris* arises as in Man. But it has only two insertions—into the tarsus and conjunctiva—instead of three. It is supplied by the third nerve as in Man. The frontal nerve is far internal to it. The *superior oblique* arises as in Man, and the trochlea is well developed. Its long, fan-shaped tendon is inserted into the eyeball distinctly to the outer side. It passes under the superior rectus. The fourth nerve supplies it by three branches. The *rectus superior* arises, and is inserted, as in Man. As its insertion the ocular surface plays upon the anterior border of the

superior oblique. It passes through an arch formed by the capsule of Tenon. The *rectus externus* arises by two heads and is inserted as in Man. It is broad and moderately thick. The third nerve crosses both heads instead of passing between them. The fourth nerve passes over both heads as in Man. And the sixth nerve comes out between them before sinking into their ocular surface. The naso-ciliary nerve also crosses both heads. The *rectus internus* is broad and thick, and its attachments are as in Man. Its nerve, from the superior division of the oculomotor nerve supplies it by several twigs. The *inferior oblique* arises by fleshy and tendinous fibres from the floor of the orbit a quarter of an inch external to the nasolachrymal duct. It is not spread out as in Man, but remains as a thin belly, which is inserted farther back into the sclera close to the entrance of the optic nerve on the postero-lateral aspect of the ball (text-fig. 27). The *rectus inferior* is as in Man. It is, therefore evident that the recti are almost as in Man, but the obliques and levator palpebræ differ.

The nerves and vessels are described in other sections of this paper.

The *capsule of Tenon* is very strong.

The *ophthalmic veins* are as in Man.

On pulling the eye forwards it was seen that the fascia lying next to the eyeball was seen to be well developed, and almost free from fat. The globe itself is relatively smaller than in Man, but the ophthalmoscopic appearances are very similar in both, as pointed out by Lindsay Johnstone (70).

Auditory Apparatus.

It is well known that the auricle is less degenerate in the Chimpanzee than in Man and the other Anthropoids. And from the numerous accounts which have been published it appears that the auricle is one of the most variable parts of the external anatomy of the Chimpanzee. Its very complete form in my specimen is shown in Plate I. fig. A. It has few hairs, and Wallis (58) pointed out that it has this feature in all examples. Darwin (16) noted that neither the Orang nor the Chimpanzee move their auricles, and I was unable to detect any movements on any occasion when I made observations in the Ape House in the Gardens. In Plate II. fig. B it is shown how the auricular cartilage is very complete, and it has a wide, thin peripheral rim. But the human auricular cartilage is a totally different thing. I was unable to detect intrinsic muscles in the cartilage.

The tympanic membrane cannot be seen through the ordinary aural specula, for it lies at the end of a long, bony external auditory meatus.

The Eustachian tube has no well-marked torus round its pharyngeal end, and I did not detect a salpingo-pharyngeus muscle.

Doran (71) pointed out that the auditory ossicles, taken as a whole, resemble those of Man more than do those of the Gorilla and Orang. But in these Anthropoids the ossicles resemble those of Man more than do those of the Chimpanzee in a few points. In the Chimpanzee the malleus is more human than those of the Gorilla and Orang. "In the shape of its head, which projects markedly forwards, and in the nature of its articular surface, of which the outer segment is much the widest, it approaches *T. gorilla* more than *Homo* or *Simia*; but in the neck and manubrium it is very human, the only difference being that the latter, in this ape, is narrower at the base, and more curved than in Man, and its well-developed processus brevis is directed upwards, and hardly outwards. In length the handle does not exceed that of our species—another prominent distinction from the other two apes. The body of the incus resembles that in *Homo*: the processus brevis is more slender, and ends in a sharp point, with no trace of any depression on it. The processus longus is rather stouter and shorter than in Man; it forms with the posterior crus a right angle. The stapes is smaller than in Man. The crura are almost equally curved; they are shorter and more slender than in Man, but wider apart at their insertion. They are well grooved towards the aperture which is wide. The base resembles that of *Homo*, though less distinctly reniform, and equally rounded off at both extremities."

The Skin and Tegumentary Organs.

As the Chimpanzee uses the extensor surfaces of his fingers in progression the skin has become modified. On the penultimate phalanges it exhibits long, oval callosities; and it has papillary ridges on its terminal ones. These ridges appear to increase during the period of growth, and Kidd (56) after describing their longitudinal direction states: "their long axes are at right angles to the line of progression of the animal. There is no correlation between the act of prehension and the direction of the ridges, though it agrees closely with the general rule which obtains in so many regions, that the ridges lie at right angles to the line of incidence of the predominating pressure on the part."

The mammae are two in number, and pectoral in position. The umbilicus was very faint in this specimen.

The following account of the comparative histology of the hairs of the Anthropoid Apes has been written by Mr. F. Martin Duncan, F.R.M.S., F.Z.S.:—

The hair of the Chimpanzee is lank, coarse in texture, and jet black in hue. Microscopically it presents certain interesting features. The cuticular scales are well marked, narrow, and of the imbricate-ovate type characteristic of the Anthropoid Apes, and in contour bear a closer resemblance to *Gorilla* than to *Simia*. In the cortex, between the cuticular scales and the medulla, the pigment granules are very numerous, opaque, and

tend to coalesce in short, regular lines. The medulla is continuous, homogeneous, and densely pigmented. The hair shaft is cylindrical. (Pl. III. fig. A.)

A transverse section of the skin, passing across a hair-follicle, shows the thick outer and inner root-sheath, with the layers of Henle, and of Huxley, both well developed; while the mass of elastic tissue closely surrounding the hair-follicles presents a very striking appearance (Pl. III. figs. B and C).

PATHOLOGY.

Nothing is known of the diseases to which the Chimpanzee is subject in its native surroundings. In captivity in Europe it usually succumbs to diseases of the respiratory or digestive organs. Some animals die from generalised tuberculosis, or from osseous and arthritic changes after many years in confinement. The following table, compiled from the death reports, shows the causes of death and duration of life of animals which have been in the Society's Gardens since 1882.

No.	Date of Death.	Life in the Gardens.	Cause of Death.
1.	7. 5. 1882	1 month.	Ulcers of tongue. Viscera healthy.
2.	8. 6. 1883	16 days.	Pneumonia.
3.	29. 10. 1883	5 "	Typhoid fever*.
4.	22. 6. 1884	1 month.	Bronchopneumonia. Ascites.
5.	4. 11. 1886	4½ months.	Acute bronchitis.
6.	20. 3. 1889	11 days.	Pneumonia.
7.	1. 6. 1889	1 year, 7 days.	Bronchitis.
8.	15. 4. 1891	2 years, 4 months.	Pneumonia.
9.	28. 8. 1891	7 " 10 "	Pneumonia, peritonitis (TB.).
10.	15. 11. 1891	4½ months.	Pneumonia.
11.	23. 9. 1895	1 year, 5 months.	Hypertrophied liver. Ascites.
12.	17. 11. 1895	8 months.	Bronchitis. Pneumonia.
13.	12. 12. 1896	5 months, 9 days.	" "
14.	13. 12. 1896	1 year, 2 months.	" "
15.	1. 6. 1897	4 days.	Not opened.
16.	27. 9. 1898	3 "	Debility.
17.	8. 10. 1898	1 year, 5 months.	Bronchopneumonia.
18.	3. 12. 1899	11½ months.	Not examined.
19.	6. 12. 1899	7 months.	" "
20.	24. 3. 1900	4 years, 1 month.	Chronic pneumonia.
21.	16. 10. 1901	10 months, 1 week.	Pneumonia. Hepatic congestion.
22.	9. 1. 1903	7 months.	Prolapsus ani. Killed by order.
23.	4. 12. 1904	1 year, 10 months.	Bronchitis.

* Authority J. B. Sutton.

<i>No.</i>	<i>Date of Death.</i>	<i>Life in the Gardens.</i>	<i>Cause of Death.</i>
24.	20. 3. 1905	1 month.	Generalised tuberculosis.
25.	16. 1. 1906	3 months, 3 days.	Colitis.
26.	24. 4. 1907	4 years, 0 months.	Trauma.
27.	7. 9. 1907	2 " 5 "	Ulcerative colitis.
28.	19. 11. 1907	3 years, 12 days.	Colitis. Enteritis.
29.	6. 7. 1908	1 year, 2 months.	Bronchopneumonia.
30.	8. 7. 1908	3 years, 2 months.	" "
31.	20. 12. 1917	4 " 7 "	Fracture of skull.
32.	9. 1. 1918	7 " 3 "	Pneumonia.
33.	1. 8. 1919	10 " 10 "	Chronic arthritis.
34.	7. 10. 1922	2 " 6 "	Pneumonia.

It has been shown by Metschnikoff, Roux, Neisser, and Lassar that the Chimpanzee is more susceptible to the virus of syphilis than any other Ape or Monkey. The primary lesions appear in thirty days after inoculation; the secondary symptoms develop after a further period of more than thirty days; but tertiary signs have never been observed.

All experimental inoculations with the gonococcus have failed to produce a result.

Keith has collected papers by Owen (75, 76), Schmidt (77), Rollet (78), and Meyer (79) on the pathology of the Chimpanzee. And the works of Ehrlich and Hata give accounts of the transmissibility of yaws to Apes; but the actual Apes employed have not been mentioned.

I desire to express my thanks to Dr. Doreen Stranger, Dr. J. H. James, Miss Kahan and Messrs. Aourounin, Henderson, Meneces, and McCormick, students in the Anatomy Department of University College, for their assistance in the dissection of the animal described above.

COMPARISONS WITH MAN.

The Chimpanzee resembles Man in a general way in form and structure, but it differs from him in many respects. Some of the differences are associated with habits and diet; others are dependent on differences in the size and complexity of the brain; and others again are the outcome of different developmental processes.

At a certain stage the fetuses of the Chimpanzee and Man have several features in common, but the subsequent developmental changes—both intrauterine and extrauterine—proceed in different directions. In the Chimpanzee they are marked by a progressive increase in certain parts, such as the hair and facial skeleton. In Man, on the other hand, they are characterised by suppression; but the power to develop farther lies dormant.

The suppressive agents are the various ductless glands. When they are diseased the suppressive power is removed, the latent power reasserts itself, and Man assumes certain ape-like characters. Man, in fact, retains more foetal characters than the Chimpanzee. The most distinctive character of the human foetus is the foot, for it has never been seen with the hallux projecting from the postero-mesial aspect of the sole.

The Chimpanzee differs from the white races of Man in its pigmented, hairy skin, its thick lips, and its overgrown facial skeleton, which exhibits large supra-orbital crests, prominent zygomata and malar bones, prognathism and large mandible. But diseases of the ductless glands cause Man to assume one or more of these characters, for they remove the suppressive agencies. In Addison's disease of the supra-renal capsules the skin becomes pigmented; and in the various disorders of the pituitary body, so beautifully monographed by Cushing (15), the lips thicken, the skull exhibits large crests, zygomata and malar bones, maxillary or mandibular prognathism occurs, and there is a variable amount of hirsuties. The extremities also become large and clumsy. Many of these conditions are present as the normal characteristics in the lower races of Man; and one of the most prominent features in the skull of *Homo rhodesiensis* is the enormous development of the supra-orbital crests.

At a certain stage in development the foetuses of all Primates have external genital folds. In the human foetus they continue to develop and form the labia majora and mons veneris, and they bury the labia minora and clitoris. In the lower Primates they disappear and the clitoris is exposed on the surface. But the Chimpanzee exhibits an intermediate condition. The mons veneris is slight, and the labia majora are represented by two slight elevations of the skin over thickenings of the subcutaneous tissue (Pl. I. fig. C). The chief difference between the Chimpanzee and Man is the absence of the hymen. In diseases of the ductless glands the organs atrophy in Man.

The biochemical reactions of the blood show that Man is related to the Chimpanzee and other Anthropoids, and it is evident from the above that the actions of the ductless glands have altered the appearances of these relatives in a pronounced manner. Bolk (7) has shown that the suppressive action has not only influenced the somatic features of Man, but it has retarded his development and succeeding life phases. He believes that the ancestor of Man changed his diet from frugivorous to omnivorous, and the change may have been the factor which evoked the suppressive action of the endocrine organs.

The compressed head appears sunk between the shoulders, for the neck is short. It is also more rigid than in Man. This arrangement throws no obstacle in the way of the long arms, and the shortness of the neck may be designed to give the powerful levator anguli scapulae and levator claviculae a very strong fixed origin.

If some object is held above the animal's head one can see that there is a considerable upward movement of the eyeballs, but the head does not move much. And the greater upward movement of the eyes compared with that in Man is effected by a more posterior attachment of the inferior oblique muscle.

The Chimpanzee uses its arms as hook-like suspenders, but the diminutive thumb is of no great use for suspension. The newborn child can, it is well known, support the weight of its body for a half to two minutes in a similar manner. Its fingers reflexly assume this position if one places his index finger in its palm.

Much has been written about the attitude of the Chimpanzee, but the conclusions, in several instances, have been drawn from the study of dead material, or from the observation of sluggish animals moving clumsily across the floors of their cages. Those who have observed Chimpanzees in their natural haunts testify to their activity and agility; and I have been fortunate in being able to examine a male Uganda Chimpanzee, lately arrived at the Gardens, which still exhibits much of its original activity. It runs about actively, using its arms and legs almost equally; it occasionally uses its foot as a spring-board; and it swings about on the branches in its cage very actively.

Anatomical descriptions state that the Chimpanzee keeps its knees semi-flexed and give that as one of the factors which prevent the animal from assuming the erect attitude. And Humphry (26) states that one cannot fully extend the knee without doing violence to the muscles. If, however, the living animal is examined a different state of affairs can be observed; but the observations must be long and frequent. I observed the active animal mentioned above extending its joints fully, both during active progression and while standing up and holding on to the bars of its cage. Two young animals were then examined during their active movements, and the same conditions were observed. After studying the active range of movement I examined the passive movements in two other young animals, and I found that I could easily extend the knees; but the curvature of the upper end of the tibia gave the leg an apparent slight flexion even when the knee is lightly extended. It is, therefore, evident, from the results obtained on these five living animals that the knee-joint can be fully extended. The position of semi-flexion is, however, more comfortable in the Chimpanzee, as it is in Man, and an animal which becomes sluggish in captivity will develop stiff joints, so full extension of the knee will then become impossible, either actively or passively. And I believe that some anatomical accounts have been based on the examination of limbs so affected.

If the animal were deprived of its arms it could not stand upright like Man, but it can under momentum be erect for a short period; I have observed the active animal mentioned above

run for a few paces in the erect posture. The maintenance of the erect attitude in Man is effected by a very complex and beautifully adjusted nervous, muscular, and osseous mechanism; but many factors co-operate in the Chimpanzee to make it quadrupedal when on the ground. In the first place, the centre of gravity is high, for the greatest weight of the body is nearest the arms. The animal will naturally fall to the ground unless it uses its arms as supports. In Man, on the contrary, the centre of gravity is low down near the supporting legs. As distension of the abdomen by food and pregnancy throws the line of gravity farther forwards in Man, the effect of similar conditions on the Chimpanzee will make the arms all the more necessary as supports. In the second place, the muscles of the back are more rigid in the Chimpanzee, so they are not employed as in Man for adjusting the balance to suit awkward positions. Thirdly, the arrangement of the bones and joints of the pelvis and lower limbs in the Chimpanzee is such that the lower limbs cannot be converted into strong supporting pillars. Finally, the muscles are not so subdivided as in Man, so the movements are more massive. There is not the fine co-ordination of movements which Man obtains through a highly organised brain, a delicate and complex nervous mechanism, and a subdivided muscular system, whose elements can group themselves to produce complex actions.

The Chimpanzee experiences joy and anger, and young ones manifest jealousy if their companions are petted. It expresses these emotions by grimaces instead of fine facial expressions. The lips and cheeks exhibit gross movements, and many teeth are exposed. The reasons for this are the coarseness of the platysma and its very intimate union with the labial muscles; and the latter are coarse, fused, and devoid of fine subdivisions.

The muscles of mastication are built on the same plan as in Man, but they are more powerful. And the prognathism makes the levatores and tensores palati more horizontal than in Man.

The columns of the erector spinæ are coarser than in Man, and pass farther up into the neck. And the shortness of the neck almost obliterates the sub-occipital triangle.

The muscles attached to the shoulder girdle are so arranged that the arm can be moved far backwards. In addition to the usual elevators, which are more powerful than in Man, there is a levator claviculæ. The nerve supply to the rhomboideus, levator scapulæ, and first part of the serratus magnus is very rich. The Chimpanzee has also a dorso-epitrochlearis.

If several animals are examined it is seen how the pectoralis minor writes its evolutionary history.

There is considerable fusion between the muscular bellies of the flexors and extensors of the wrist and fingers. The flexor carpi ulnaris is more bulky than in Man, and it is inserted into a

very large pisiform bone. The trapezium, on the other hand, is small, and there is no os centrale as in *Simia*. The minute flexor longus pollicis is an offshoot of the tendon of the flexor profundus to the index. The palmaris brevis is large, the first and second lumbricales are connected by a muscular slip, and there are six palmar interossei. Still those anatomical differences are not sufficient to show that the hand of the Chimpanzee is not such a marvellous mechanism as that of Man.

The muscles of the abdominal parietes are very strong, for they act as flexors of the trunk, and they support the abdominal viscera when the animal is walking. A pelvic floor is present, but there is no true central point of the perineum, which plays such an important part in supporting the uterus in woman. The vulva and anus are behind a line connecting the anterior extremities of the ischial tuberosities, but a corresponding line in woman passes between the vulva and anus.

The quadratus lumborum is shorter than in Man, and is strongly fused with the iliacus, and the latter is longer than in Man. The glutei are less than those in Man, but the maximus has a longer insertion. The glutei and other thigh muscles exhibit a considerable degree of adhesion, and some of the thigh muscles are inserted into the fascia over the muscles of the leg. The scansorius is absent in Man. The adductors form a powerful mass, and they help to keep the inverted foot against a tree in climbing; from the backward projection of the ischium the adductor magnus is a powerful extensor of the leg in leaping. In the muscles of the leg it is interesting to note the doubling of the tibialis anticus and the absence of a tibial head of the soleus.

Anatomical literature contains many speculations as to the nature of the foot of the Chimpanzee. Cuvier, Blumenbach, and Owen, and in later years Huxley (27), Humphry (26), and Embleton (19) have proposed different views. A survey of their writings shows that it has been regarded as a foot, a hand, or a compromise between them, that is a chiropodous structure. To settle this question it is necessary to consider the extremities from the anatomical and physiological points of view, and it is necessary to examine them in several animals. Using the human hand as a standard, it is, in the first place, necessary to see how it differs from a fore-foot. Humphry (26) points out that the elongation of the phalanges and the shortness and opposability of the pollex are the characters which transform a fore-foot into a hand. In the case of the terminal part of the lower extremity many of the myological and osseous features are characteristic, not of a hand or a foot, but of a hind limb. So we must look to the characters of the digits and hallux to determine the nature of the part in the Chimpanzee. Comparing the measurements in

the animal whose anatomy is described in this paper with those in Man the following results are obtained:—

	<i>Chimpanzee.</i>	<i>Man.</i>
End of heel to tip of middle digit . .	7.4 ins.	8.4 ins.
Hallux and its metatarsal bone	4.0 „	4.5 „
Hallux without metatarsal bone . .	2.2 „	2.3 „
Length of metatarsals 2-5	2.0 „	2.5 „
Length of phalanges:—		
second digit	2.5 „	1.8 „
third „	2.8 „	
fourth „	2.5 „	
fifth „	2.3 „	
Total length of second digit	4.5 „	4.3 „

It is thus seen that in the Chimpanzee the phalanges of digits 2-4 are more than a third of the length of the foot, but the fifth digit is less than a third; but in Man they are less than a quarter of the length of the foot. The hallux in the Chimpanzee is shorter than the other digits, but it is slightly longer than them in Man. In the Chimpanzee the relative lengths of the digits are as in a hand, and the digits act towards or from a line passing through the middle digit; in a foot the basal line passes through the second digit. All these data show that the pelvic extremity in the Chimpanzee is terminated by a hand. And if the grasping action of the human hand be taken as a pattern it is even more effective than the hand which terminates the pectoral extremity. The hind hand is not employed as an exploring organ, and its grasping action is chiefly an aid to progression, so Humphry (26) thinks that the term "chiropod" best describes it. And he makes the following important statement:—"Whichever term is used it must not be forgotten that the configuration on which it is based is not peculiar to the monkeys, but is common to them with some other tree-roving animals, such as Iguanas and Opossums. In human beings, who are born without arms, the foot can be educated to take the place of the missing hands. And medical literature contains records of such persons who could grasp objects and carry out complex movements, such as painting, with their hallux and foot digits. These cases have been adduced by some writers to prove that the leg of the ape is also terminated by a foot. They do not really disprove the views stated above for:—1. The proportions of the hallux and digits to each other and to the whole foot are normally foot-like; 2. The middle line, or basal line, runs through the second digit; 3. The hallux can be abducted, but it is not really opposable; 4. The prime work is to act in conjunction with the other characters of the leg in forming a strong supporting basis for the body.

The joints between the occipital bone, atlas, and axis differ from those in Man. The inferior crus of the cruciate ligament is absent, and there are additional strengthening bands. No

ligamentum nuchæ is present. Owing to the greater forward projection of the odontoid process, the check and middle odontoid ligaments are more horizontal than in Man. The articular processes cause more locking of the atlas and axis. The head has a much more limited movement, and this is accompanied by a greater upward mobility of the eyeballs. The carpal ligaments are more complex than in Man. And the construction of the joints of the pelvis and leg are such that the animal cannot stand stiffly in a fully erect attitude without holding on to branches above it.

The mouth differs from that in Man in the greater number of palatal rugæ and in the characters of the tongue, although Wood-Jones states that the tongue is like that in Man. The pharyngeal musculature is similar in both, but the Chimpanzee has the larger sinus of Morgagni. Man has only two muscular coats in his œsophagus, but the Chimpanzee has an additional inner longitudinal coat in its upper part. Man has three muscular layers in his stomach, but the Chimpanzee has only two; and the inner coat is composed of oblique or circular fibres in different parts. As regards the intestinal tract the most striking differences are found in the rectum. The Chimpanzee has five enormous valvulæ conniventes running completely round it, and the columns of Morgagni are very prominent longitudinal folds running down to the lower end of the anal canal. When the anus is dilated these columns are seen at once. No valves of Bull connect the columns as in Man. The anus is prominent as the gluteal regions are small, whereas the reverse is the case in Man.

The amount of lymphoid tissue in the intestinal mucosa is less in the Chimpanzee than in Man.

The liver and pancreas are practically the same in both.

The heart is small in the Chimpanzee, but its structure is as in Man. The branches of the aortic arch take one of two forms, and one of these varieties is as in Man. The subclavian arteries give off well-marked spinal branches, and the branches of the axillary artery come off as in the Cercopithecidae. No arterial anastomoses exist round the scapula or elbow joint as they are in Man. The vessels in the forearm form long parallel branches, much as in the Lorises, and there are three palmar arterial arches, whereas Man has only two. The branches of the abdominal aorta are fewer than in Man; and in my specimen the femoral artery gave off branches which combine those of the external iliac and femoral arteries in Man. The femoral artery gives off a saphenous artery to the foot, and the anterior tibial artery courses differently from that in Man.

In the venous system the chief differences from the condition in Man are the freer intercommunications between the parts of the portal circulation, the absence of a saphenous opening, the ending of the cephalic vein in the lower end of the brachial veins, and the presence of a large brachial vein instead of two *venæ comites* of the brachial artery.

The lymphatic system is characterised by a doubling of the thoracic duct; and the groups of glands are much fewer than in Man.

The ductless glands generally resemble those in Man. But the thyroid is a long, narrow U-shaped organ instead of being composed of an isthmus and two lateral lobes. The vascular supply is interesting in my specimen, but I am unwilling to regard it as the normal condition till other material becomes available for examination.

The lungs are divided into the same number of lobes as in Man, but they are subdivided differently. The trachea and bronchi are as in Man, but the larynx differs in some points of structure, and in the possession of a large air-sac. Vrolik has shown that they are largest in the aged, and it is possible that this fact is correlated with weaker muscles at that period of life.

The external generative organs have already been alluded to. The internal organs are built on the same plan; but the round ligaments are relatively much thicker than in the human condition. They may play a more important part in fixing the uterus than they do in woman. The vestibule is very small, and the meatus urinarius opens within the vagina.

It is sometimes stated that Man and *Ateles* are the only Primates which possess more than one renal papilla. But that is not the case, for I have seen kidneys of Chimpanzees with three to six papillæ. The left renal artery is peculiar in my specimen for it anastomoses with lumbar arteries, whereas the renal arteries are end-arteries in Man.

In its origin from the femoral artery, and its course up through the femoral sheath the obturator artery in my specimen courses as in one form of abnormality in Man.

Man differs from the Chimpanzee in being himanous and bipedal, and in the possession of those higher mental powers which we designate by the name of the Soul.

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EXPLANATION OF THE PLATES.

PLATE I.

- Fig. A. The external ear.
B. The auricular cartilage.
C. The external generative organs. Letters in text.

PLATE II.

- Fig. A. The turbinate region. Letters in text.
B. The antrum of Highmore. Description in text.

PLATE III.

- Fig. A. The hair shaft.
Figs. B & C. Sections through the skin and the root of a hair.



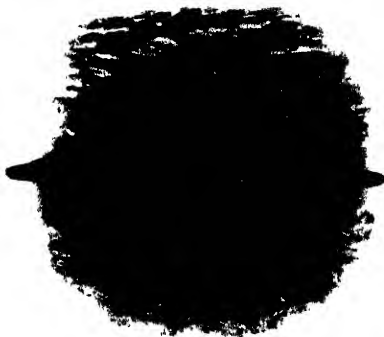
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ELEPHANT-SEALS OF KERGUELEN LAND.

23. The Elephant-Seals of Kerguelen Land.

By T. P. A. RING*.

[Received November 21, 1922: Read March 6, 1923.]

(Plates I. & II.†)

The hunting of the Elephant-Seals of the southern hemisphere, on a scale which threatens these interesting animals with extinction, began at the South Georgia group of islands in the South Atlantic, which are under the jurisdiction of Great Britain, and form part of the Falkland Islands dependencies.

A factory for whaling was established in the year 1905-6, by a Norwegian, Captain C. A. Larsen, of Antarctic exploration fame. This enterprise proved so successful that other establishments for utilizing the larger cetacea were soon erected. As a "side-issue," the capture of the Elephant-Seals was also included, and in consequence their numbers must have been so reduced that, unless the British Government introduce legislation forbidding the capture of these animals for, say, 10 years, they will become extinct. Such legislation ought also to embrace the protection of the Fur-Seals.

At the Crozet Islands, situated in the South Indian Ocean, and which are under the jurisdiction of France, a Norwegian steam sealing-factory made a great haul of Elephant-Seals in 1907, and three years later a French floating-factory cleared the beaches of the remnant left by the Norwegian vessel. In the year 1908 a Norwegian company established a whaling factory at Kerguelen Land in the South Indian Ocean. This also is a possession of France, and in the course of four years (1909-1913) Elephant-Seals were killed in such great numbers that, unless the Government of France takes steps for protecting them from destruction by enforcing strict protection, say for 10 years, their extermination is practically certain. The Elephant-Seals and Fur-Seals of Marion, Prince Edward, and the Crozet Islands should be similarly protected.

The transport vessel of the Kerguelen Whaling Company, the S.S. 'Jeanne d'Arc,' arrived at the Island with all the paraphernalia for establishing a whaling factory, on the 29th of October, 1908, coming to an anchor in Gazelle Basin, a fine harbour situated centrally on Kerguelen Land. During the fortnight following, the vessel visited a great many bays looking for a suitable site for putting up the factory, which finally was established to the west of Long Island in Royal Sound, thus named by Captain James Cook in 1776. On every sandy beach

* Communicated by Sir S. F. HARMER, K.B.E., F.R.S., F.Z.S.

† For explanation of the Plates, see p. 443.

of any extent a huge bull Elephant-Seal, the beachmaster of the old-time sealers, was found to be in possession of a herd comprised of females and youngsters—dams and pups—whilst on smaller beaches, and lolling about on the grass-covered plains above the beaches, were flocks of male Elephant-Seals of various ages and dimensions, termed “pods” by the sealers.

The dams were all brown in colour, measuring from seven to about eleven feet in length, and rather emaciated after suckling their pups, who were in splendid condition, almost bursting with fat, and covered with a pretty silver-grey coat of short hairs. The beachmasters were most imposing looking, compared with their offspring, among which the young bulls measured as much as seven feet in length, whilst the females were no more than five feet long. The guardians, or “sultans,” of the harems were, in most cases, dark brown, like the dams; though some were dark grey in colour. On some beaches a solitary, dun-coloured bull was seen, who, like the beachmasters, was scarred from many a fight; and among the “pods” of variously sized grey bulls, fighting was the order of the day, combats being waged at all hours if the sun was not out, and for the mere pleasure of battling; the hoarse bellowings of struggling bulls being audible at night as well.

In the course of a week several anchorages on Kerguelen Land were visited by the S.S. ‘*Jeanne d’Arc*,’ and about the 6th of November the beachmasters were observed to be very much on the alert to prevent the dams from abandoning the pups: placing themselves between their harems and the water. Whenever a dam tried to pass, the bull simply crushed her down, and he would even administer a bite; but whilst he was thus engaged another dam would watch her chance, and slip past him into the water. With angry bellowings the beachmaster would try to intercept the runaway; but no sooner did the dam kept down by the bull feel the pressure diminish, than she, in her turn, slipped away, and there the baffled Sultan stood, bellowing forth his rage at the escape of his odalisques.

The beachmasters were found to measure from about 18 to 21 feet in length; and had always a well-developed proboscis, which is an enlargement of the snout more nearly resembling that of the tapir than the trunk of an elephant; whence, however, is derived the name “Sea-Elephant.” As long as a bull is undisturbed this “proboscis” hangs flabby and limp to one side of the jaw; but when excited, or roused to anger, it becomes rapidly inflated with air and enormously enlarged, the process of inflation being accompanied by short snorts. The bulls, when fighting each other, are very careful to prevent the trunk from being seized, contracting and raising them, as far as possible, out of harm’s way. The dams are entirely devoid of this enlargement of the nose, which is a sign of sexual maturity in the males, and is most pronounced during the rutting period; while it is perceptible in the pups when only seven to eight weeks old.

By the 10th of November only a few cows were left, and it had been noticed that each had but one pup to suckle. In several harems there were a few without youngsters; and these were assumed by us to have been unfecundated. As late as the 21st of the month a dam was seen to have come up to the beach to suckle her pups, and as the youngsters were increasing in fatness for some time after the disappearance of the mother seals to recoup their strength after the exhausting strain of suckling, the dams had evidently returned, now and then, to the beaches before finally abandoning the pups. After Christmas the cows began to reappear, all being in fine condition after their voyage of recuperation, some arriving even earlier, and they now went far up on land to loll about among the bulls changing their coats, and growing slim again, until the month of April when the great exodus of the Elephant-Seals took place.

In the month of November the weather was fairly fine; and the pups which, on the departure, or rather the disappearance of the dams, had withdrawn from the beaches and collected on the green slopes above, were seen by the end of the month to approach the water again. The beachmasters had remained to guard their youngsters, and were very prompt to come to their assistance when teased by us. Indeed those bulls, which had been harassed and troubled by the men, had at last become quite furious, so that the sight of a man was sufficient to drive them into a towering rage.

Whilst lying on the slopes, the pups were seen to charge each other in clumsy hops, and express their feelings in a kind of hooting when catching each other up. The male pups also tried to fight one another; but on raising their fat, round bodies they generally tumbled over: and when teased the nose would be puffed up twice its original size. The quivering of the muscles of the face gave the otherwise docile physiognomy of these youngsters quite a ferocious aspect.

They had decreased considerably in fatness, though grown in length when mustering on the beaches about the 3rd of December: and by the 10th the beachmasters, who were very much reduced in bulk, and who occasionally would disappear for a couple of days, doubtless to seek some food, took their departure with their offspring. In the month of February the pups reappeared, the males having grown to a length of about nine feet, whilst the females hardly measured more than seven feet in length.

The "pods" of bulls or bachelor seals, which on our arrival were seen on the beaches and the flats above, disappeared at various times to feed themselves up, and on their return, after about two months' absence, they resorted far up on land, to spend the remainder of the summer basking in the sunshine on the slopes and plains above the beaches, shedding their hair and growing thin again; many were seen in the miry troughs or oval hollows made by generations after generations of seals, and others

in bog-holes, chiefly above Cape Digby on the lowland, where the animals were wallowing about like so many crocodiles. Fighting would be the usual pastime in rainy weather; but with the sun out, they were chiefly engaged in throwing up mud and sand on to their backs with a backward sweep of the fore-flippers, so that the body was entirely covered. It being too hot to fight, they would also chase each other about and play at pairing. Instead of going up the slopes some seals seemed to prefer lying among the boulders forming the talus, at certain parts of the coast-line, and the grey, clumsy shapes of the animals were difficult to distinguish from the boulders.

By the end of March, and in the beginning of April 1909, the Elephant-Seals were coming down to the beaches again: travelling leisurely, and having bouts of contests as shown by their tracks and the downtrodden mud.

The gathering of the clans took place on the beaches, the seals departing in companies on their four to five months' tour of migration, but unfortunately it was impossible to ascertain if the males and females travelled together or separately. By the 1st of June the beaches had become deserted; but some seals, males and females, were seen to remain behind and winter over, the animals probably suffering from some disease or other. Snow did not affect them much and they were lying on the beaches as well as in the shallows, covered with snow, and looking like so many logs of timber. When asleep in the water the heads of the seals were sometimes visible, and at other times submerged, and for hours they would remain asleep without stirring. When a snap of frost set in the beaches were deserted, the temperature of the water being more congenial than that of the air.

It has been mentioned that after their tour of recuperation the seals were in splendid condition: and that they travel far has been proved; the late Captain Robert Falcon Scott having observed Elephant-Seals at South Victoria Land in latitude 77° 50' South, during the Antarctic summer. The animals fed themselves well when travelling, as shown by their sleekness when hauling on land again; and when returning after their five months' voyage of migration, the seals were in even a better condition. Their route is unknown, as no congregations of seals have ever been met with by vessels "running the easting down" in the latitudes of the roaring forties, and the probability is that these animals resort to the regions of the pack-ice during the winter, unless they perform a round voyage, like the hump-back whales, or follow the route of migrating fishes. They may, of course, visit unknown feeding-grounds; but the pack-ice seems a more likely region where an abundance of food may be found, and the seals are safer from their chief enemy, the prowling *Orca gladiator*. Several of these ferocious "Dolphins" were seen cruising in the fjords of Kerguelen Land, and many a seal had deep cuts which only could have been inflicted by a powerful beast like the "Killer-Whale."

Several Elephant-Seals were seen during the winter in the various anchorages resorted to by the whalers in bad weather, a few Crab-Eaters and one Ross-Seal, as well as a small number of Sea-Leopards, also having been observed, and specimens secured for Museum purposes.

On the 28th of August 1909 three large, grey bulls hauled up at Swain's Haulover, a neck of land separating Swain's Bay from the fjord to the west of Long Island, in Royal Sound, where the whaling factory had been established, and about $2\frac{1}{2}$ miles distant from the latter. The weather had been, and still was, abominable, and the seals disappeared again. Tracks in the snow showed that they, or some others, had been up a day or two earlier, but none were seen again until the 3rd of September, when several "hauled up" at Swain's Haulover, as well as in Royal Sound, and at Greenland Harbour Haulover, which separates this harbour from an arm of Royal Sound. The new arrivals drove the bulls that had wintered over, and which were very thin, compared with the others, away to the corners of the beaches, or compelled them to seek another beach, and they then commenced to battle between each other for the supremacy, which meant the possession of the beach. The weather was most uncongenial however, the thermometer only registering $30\frac{1}{2}^{\circ}$ F., though the sea-water was much warmer. On this account the fights were rather half-hearted, and the water was preferred.

In the course of a week an increasing number of large bulls hauled up: and on the 11th of September a few dams reappeared. The battles between the rival males now began in real earnest, the arrival of the females adding a zest to what previously seemed a mere pastime. The combats now assumed a sanguinary and decisive character. It was always bull to bull, and whenever a large bull without provocation attacked a weaker one, others would come to the assistance of the latter, and hurl themselves at the bully. The duels were fought in the shallow water until the bulls were, so to speak, sorted out in pods of equal strength and dimensions, and at last only one or two remained, the others taking themselves off, and away from the victorious bull, who took up his position among the dams. At Swain's Haulover two fine bulls lingered in the shallow water without ascending the beach. Both had come out as victors over their rivals, and both had had several trials of strength.

What may be called real water-pantomimes had been witnessed by us: the pelting of the sundry fighting bulls with stones having nonplussed the animals to such an extent that, when a stone hit one, the beast would thrust his head into the water after the stone, and on finding what had given him the stinging blow, he looked round in a dazed way and next furiously went for the nearest of his compeers.

It was rather puzzling to see that neither of the two bulls took possession of the beach, although an increasing number

of dams were hauling up, but on the 14th of September the riddle was solved—our friend of last year, the Sultan, made his appearance.

This special bull, and also one in Seelhorst Harbour, near Gazelle Basin, on the east coast, had been the objects of much harassing by our people, both being fine brown specimens about 20 feet long, and both possessing a mutilated proboscis, which distinguished them from their confrères. No sooner did the Sultan of Swain's Haulover, as he had been named, perceive his tormentors of the previous season than he made for us in eager strides, and a scene followed similar to others that had taken place, and probably remembered by the bull, as no provocation whatsoever had been offered by us, the remembrance of last year's harryings rankling in his memory no doubt.

Hurling his ponderous body along, the dark brown, eager bull, without uttering a single snort, evidently had the intention to run the object of his attack over and crush it, and great was therefore his surprise when it disappeared, the man in front having quickly slipped aside. The discomfiture of the beast was apparent as it came to a sudden stop, the inflated proboscis dropping, and a loud snort being emitted. Raising himself on his fore-flippers the bull lifted his head with the snout pointed skywards, and, looking over his back and turning his head slowly from one side to the other, a searching glance was directed backwards and sideways. The astonishment of the bull was great when he saw his enemy standing behind him, so to speak, and on getting a smart blow from a stick on his hind-flippers his surprise and disappointment gave place to a most sudden outburst of fury.

With bulging, blood-red eyes, and inflated proboscis trembling, a succession of stentorian snorts and gurgling roars came from the vibrating snout and open mouth of the bull; and on getting a second stinging cut he flopped down and curved his back, whilst at the same time the hind-flippers were thrown up, opened out, and swung to one side, imparting a momentum to the body which, pivoting on the fore-flippers, was turned with a grand sweep in almost a semicircle until he was again facing his adversary. He was undecided what to do it seemed; but a blow on the head roused him to action, and with a magnificent motion he rose from the ground, towering up to a height of 10 feet, and looking most imposing as he thundered forth his fury, which was genuine enough, and with which his whole body was shaking.

It is in this magnificent posture that the battling bulls pose, for some seconds, when challenging each other to combat; and they next hurl themselves at one another with all the momentum they can possibly impart, clashing together with a curiously soft thud, and with such force that one expects the oil to squirt out of the pores of the skin. Seizing hold of each other with their fore-flippers, the antagonists sway about, attempting to gouge out an eye, or seize the proboscis, both being careful to contract this appendage, and turn it upwards out of reach. When trying

to bite each other on the sides of the neck, the animals incline their heads towards the threatened side, and the foldings produced by this movement in the skin make a good bite difficult. Nevertheless, deep bleeding gashes are inflicted, which, however, heal quickly, and rarely fester. The fight ends, as a rule, in mutual exhaustion: the bodies of the combatants finally cannoning off each other, and dropping to the ground.

At times the combat would be renewed until the weaker one gave up the fight and took himself off, gashed and bleeding, but mostly the bulls were seen to separate, unless fighting for the supremacy of the beach.

The temper of the Elephant-Seals is normally docile; and by slowly approaching a sleeping animal, and waking it up without any undue noise, one could come quite close up to a seal, and even sit on it, and scratch it with one's cane; the soft eyes, after an almost friendly glance, closing again. If frightened the pale green pupil of the eye, set in a brown iris, would become blood-red; however, a mist of tiny drops of blood gradually filling the pupil, a hue which was also assumed when a seal was angry. Tears came into the eyes when, on waking an animal suddenly, the abrupt opening of the lids exposed the eyes to the light; but when harassed a seal would also shed tears, and the pupil then changed from pale green into blood-red.

By the 20th of September the dams hauled up in force, some arriving singly, but generally they came in companies, and on the 24th the first birth took place. The weather was cold and snowy however, and only a few dams were delivered during the two following days. On the 27th and 28th the wind went northerly, with the temperature of the air rising from 33° to 44° and 52° F., and the greater part of the pups were then produced, but as late as October 7th what appeared to be new-born pups were seen in a bay on the South Coast of Kerguelen Land, though only a few, the arrival of the dams being belated.

The delivery of the pups took place close to the sea, and the travail of the dams did not last longer than about five minutes, the heads of the youngsters appearing first, and each dam only producing one pup. The loss of blood was slight, but the delivery was attended with pain, and cries of distress were uttered at certain moments, the dams facilitating the event by movements of the body. With a sweep of the hind flippers the umbilical cord, which remained attached to the youngster, was severed. It gradually dried up, and had a length of from two to three feet. The female pups were, at birth, about three feet long, whilst the males measured as much as five feet in length; all being covered with jet-black, curly hair, and presenting more the appearance of a chameleon than that of a seal.

The *paterfamilias*, as well as the other bulls, were quite disinterested in what was taking place, although they must have been cognizant of it, as their moustaches and nostrils were moving.

The growth of the pups was astonishing: day by day one seemed to notice the progress, and in about 10 days they had more than doubled their bulk and weight. No attempt was made to seize a youngster and weigh it, but on comparing the size of some of them with that of a man, the estimate was arrived at that the pups in question weighed 180 to 200 lbs.; and at birth from 65 to 80 lbs.; the largest male pups 85 lbs. There was a preponderance of females in nearly all harems, but no certain ratio could be determined. When suckling the youngster, the mother-seal reclined to one side, offering the nipples protruding through two holes—one on each side of and equidistant from the navel, as well as in line with it—to the pup, who, after having sucked his fill, painfully dragged himself, with the heavy head bobbing up and down, into the water; the dam following up and placing herself alongside of the youngster, who rested with his fore-flippers on the shelving bottom, and both animals facing landwards. When, as often happened, the slight rough of the sea drew the pup out, and he lost the support of his flippers, the head became submerged. Immediately the dam swept the youngster up, so that he again recovered his footing. If prevented from getting into the water the pups vomited the milk. According to the American authority, Mr. N. W. Elliott, in regard to the Pribyloff Islands seals, they become land-sick; digestion, which must take place while the pup is in the water, having been prevented.

In the third week after their birth the jet-black pelts of the pups changed into brown, the black curly hairs dropping out, and brown, straight hairs taking their place, the coats being thick and rough. Gradually these were changed into the pretty silver-grey coats, which the pups had when leaving the beaches on about the 10th of December, but which, on their return in February, had assumed a darker hue.

On the 17th of October the pairing of the Elephant-Seals was observed, this event taking place when the first circumnavigation of Kerguelen Land was made by us. In Thunder Harbour, near Sadole Island, on the West Coast, where a party of men had been landed to capture the Fur-Seal,—which was believed to visit this part of our domain, but which proved not to be the case, only a couple of these seals being seen, and a small one captured—a curious commotion was noticed on the 16th of October among the hundreds of Elephant-Seals that were lying on the plain above the beach. Large bulls were seen to descend, or rather to tumble down, the steeply shelving beach from the plain, gashed and bleeding, to dive into the sea and disappear; whilst other powerful beasts were coming out of the water to ascend the beach and making their way up to the plain, whence a continuous roaring of bulls was heard, and the sharp agonized yelps of pups and dams. From an island, and at a height overlooking the harbour, the plain was dimly visible through the mist; and the huge shapes of careering bulls were discernible, the animals

coming to a sudden stop amidst the harems. Fierce fights between the bulls lying outside the herd were taking place, and occasionally an immense bull was seen making his way through the seals. Waning daylight, and the necessity for finishing a rough survey of Thunder Harbour, and taking soundings, prevented a visit to the plains, but next day, in Christmas Harbour, the riddle was solved.

The S.S. 'Jeanne d'Arc' had called here on the 24th of December, 1908, in order to take a couple of Sea-Elephants to the Durban Zoological Gardens, and two pups were most unexpectedly secured, a small bull being too tough a customer to tackle. As the migration of beachmasters, with their pups, had been noticed to happen on the 10th of December, it became evident that the season's youngsters did not abandon the beaches simultaneously with their sires, but that the latter left for the most part when it suited them, to a certain extent, together with their pups.

In Captain Cook's Christmas Harbour, two fine bulls with their harems occupied the beach, separated by a space of about 500 feet. The same commotion, but on a much smaller scale than what dimly was observed in Thunder Harbour, and which up to the day before had never been seen anywhere since the arrival of the S.S. 'Jeanne d'Arc' at Kerguelen Land, was also raging among the seals lying on the beach in this anchorage, and, on getting ashore, the reason was discovered—the cows were "in heat." Fierce, sanguinary battles were fought between the bachelor bulls lying in the shallows, the water shining crimsoned in some places, while rolling bellowings mixing with the savage hootings of the obsessed beasts resounded between the hillsides. On the beach, the two Sultans were standing alert and threatening, ready to repulse an aggressor; both mutually concurring not to poach on each other's preserves, and watching the approach of the boats with evident concern. Suddenly one of them was seen to face about, pivoting his body in a magnificent sweep on his fore-flippers, and gallop madly into his harem, where he disappeared from sight, and on gaining the beach and coming through the crowd of pups and dams we found the bull serving one of the latter.

The commotion among the "water-bulls" became pandemonium. The frenzied creatures went blindly for each other, digging their sharp incisor teeth into each other, and careering about; the sound of their roars and bellowings filling the whole harbour. One, more venturesome than the others, ascended the beach and made for the nearest cow, which he tried to ravish; the unwilling harem beauty, with loud cries of distress, making her lord aware of the situation, and appealing to him for assistance. Having satisfied the call of the other dam, the harem master came bounding along, running the offender down, and crushing him with his weight so that the underlying bull screeched with terror or agony, whilst making frantic efforts to

wriggle away, in which he finally succeeded, and wobbled into the water again, so much wiser, if not better, after his futile raid.

The Sultan of the other seraglio had in the meantime driven off a slightly smaller bull after a fairly severe trial of strength, and was found lying on the ground, recovering his breath, when he spied the two-legged intruders coming along. Raising himself on his fore-flippers the bull lifted his head, and with the snout pointing to the zenith, turned his head slowly from side to side, taking a scowling look at us, and after what must have been a satisfactory scrutiny, lying down again.

On walking among the inmates of the harem, a black dead pup was found and later two more, which the prancing bulls must have crushed in their mad careering through their harems. The Sultan, probably being aware of our heavy footfall on the hard sand, would occasionally rise to have a look round, and suddenly he became alert, the proboscis, which had been hanging limp and flabby, being inflated to a size which exceeded anything previously seen. Up went the head and with the moustache bristling, and eyes turning blood-red, the bull slowly moved his head about, the proboscis vibrating, and saliva running from the open, pink, cavern-like mouth. The posture of the seal was one of tense concentration, and all at once he threw up his hind-flippers, as usual with the animals when making a grand swerve, and bounded off through his harem, the dams and pups scuttling out of the way of the prancing bull with terrified yelpings. Coming to a stop before a dam whose youngster had scrambled well out of the way, and who seemed to be waiting for her master, and inviting him by twisting her body about, the bull with a loud snort seized the dam with a fore-flipper and served her.

The bulls in the water, who fought fiercely with each other for the privilege of being onlookers, as the men said, must also have received the silent call, as pandemonium again reigned among them, until the bull had satisfied the demand of nature. Within about 45 minutes the two beachmasters served each three dams, and every time the call came from different cows. Had all six made their demand on the services of the bulls at the same time, those in the water, which were equally possessed by the pairing instinct, would have ascended the beach and satisfied the calls of the dams.

The following day the pairing of the seals in Christmas Harbour continued, and in all the bays which were visited on our return to the whaling station—when large harems were found,—the bulls were engaged in satisfying the calls of their dams, of which none were seen to be served twice. On beaches where only a few dams formed the harem no pairing was observed, this act, no doubt, having taken place before our arrival.

In Royal Sound a beachmaster had been vanquished by a bull, which had successfully contested his supremacy. The fight had

been savage, bout after bout having been fought, according to the testimony of the men from the whaling station, who had been deputed to make tours in one of the motor boats of the Kerguelen Whaling Company, to observe the seals. The two rivals had kept up the contest for nearly 40 minutes, and the beachmaster was at last vanquished. He was almost unable to move, and one of the incisor teeth had gone, the jaws of the combatants having become interlocked, and only released by the snapping of the incisor of the beachmaster. Gashed and streaming with blood, the defeated Sultan then dragged himself painfully to the beach, and dived into the water, the wake of the animal as he swam away being crimson-red. The victorious bull, who looked only a degree less frightful than his late opponent, had taken possession of the harem, that is, he simply dragged himself in among the dams, being almost spent, and went to sleep at once. Some hours later, the motor boat having in the meantime visited other harems, the bull was observed to have recovered his mettle, and was on the *qui vive* when the boat appeared, though no pairing took place as the men passed the beach on returning to the whaling factory.

The Sultan of Swain's Haulover had also had his hands full in coping with the exigencies of the situation; but had come out victorious in all contests, although one was almost a draw. Had he been obliged to wage a similar combat soon after, the men opined, he would hardly have come out of the battle with the palm of victory.

What may be termed the rutting period of the Elephant-Seals began on the 16th of October, when the inexplicable commotion among the seals in Thunder Harbour was noticed, though it may have commenced two to three days earlier, and it lasted until all the dams in each harem had been satisfied. The mature bachelor bulls, compelled by the pairing instinct, came to contest the supremacy of the beachmasters, who by right of superior strength and size, and by right of conquest of course, had occupied the beaches and were harem-masters. The dams in each harem requested the service of their masters at different times, and not simultaneously, every dam being served only once. They evidently roused the pairing instinct of their respective masters by emitting a distinctive odour, imperceptible to the human sense of smell, and a call, which also reached the water-bulls, equally possessed with the pairing instinct, and which drove them to frenzy.

During the rutting period it was seen that the beachmasters received the call not only from mature cows, with or without a pup, but also from what appeared to us to be immature females. These females were of an almost uniform size, not more than eight feet in length, of a slender shape, and born during the last week of September of the previous year. These female Elephant-Seals when slightly more than a year old are then in heat and

paired. The bulls of the same age were naturally the smallest in the herds, but had outstripped the females in growth by as much as three feet in length. Like their older confrères they were excited by the pairing instinct, fighting furiously with one another when the call of the dams was sensed by them. When only five months old these young males had been seen playing at pairing, on their return to the beaches after their first voyage of recuperation under the guardianship of their sires. Their seniors, however, also indulged in this habit, but seldom troubled a female seal, attempted overtures being promptly and indignantly repulsed.

The dams had produced their pups about the 27th of September; their fecundation took place about the 16th of October, and they would again give birth to their youngsters about the 27th of September the following year. The period of gestation is thus about 49 to 50 weeks.

On the 2nd of November the slaughter of the seals was ordered to begin, those at Swain's Haulover and in Seelhorst Harbour to be spared for further observation purposes, and the men were also ordered to spare all dams. The pups were almost bursting with fat, and most of them had changed into silver-grey coats; whilst the mother-seals were emaciated from suckling their youngsters; but the bulls were in first-class condition. By the 8th of the month the dams began to abandon their pups, having produced them about the 27th of September. Thus the period of lactation lasts about six weeks.

In the season of 1909-10 the Elephant-Seals were observed to leave the beaches, and return about the same dates as during the season of 1908-9; and be it noted, as in the two following whaling seasons, only 82 Cetaceans were captured in 1910, and about the same number in 1911-12, the Kerguelen Whaling Co. would have been obliged to go into liquidation but for the "successful" sealing of those seasons. But as a consequence, in 1913, there would only be a small remnant of Elephant-Seals left to reproduce themselves. How far this remnant has succeeded in recovering—if it has been able to recover—during the decennium which has passed since the slaughter of the animals ceased, is difficult to conjecture. It is by no means improbable that the existence of these seals has been jeopardised through the strain which the stock has suffered during three seasons' intense hunting, as all the large and virile bulls would have been killed on account of the greater yield of blubber from such individuals. Consequently only young bulls would be left, and the offspring of such animals, deficient in virility, would be of an inferior stamina compared with the old, extinct stock. It was seen by us that as much as 35 per cent. of the pups in a harem succumbed to the dangers of the first voyage of migration, and the percentage will be much greater with seals of inferior stamina and vitality. Although the capture of the animals would cease automatically

with their scarcity which rendered any venture on a large scale unprofitable, even after a close period of ten years, it is doubtful whether the Elephant-Seals of Kerguelen Land would be preserved from extinction, sickness and the dangers of migration being important factors threatening the lives of the young seals.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. Young Bulls fighting.
2. A Bull with inflated proboscis.
3. The Challenger.
4. Bull with deflated proboscis.

PLATE II.

- Fig. 1. Elephant-Seal calling.
2. Young Elephant-Seals resting on the slopes above the beaches.

24. The Skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower Neopterygian Fishes. By C. TATE REGAN, M.A., F.R.S., F.Z.S., Keeper of Zoology in the British Museum (Natural History).

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(Text-figures 1-8.)

Although a detailed and well-illustrated account of the skeleton of *Lepidosteus* was given by Agassiz in 1833 (*Poissons Fossiles*, vol. ii.), the nomenclature makes his description very difficult for a present-day student to follow, and it has been ignored by most modern authors. In his memoir on the development of the skull of *Lepidosteus osseus* (Phil. Trans. 1882), Parker has given a description of the skull of the adult fish which is in some respects less complete and less accurate than that of Agassiz. More recently Collinge (Proc. Birmingham Phil. Soc. viii. 1893) and Allis (Internat. Monatsb. Anat. Physiol. xxi. 1905) have studied *Lepidosteus* especially in relation to the sensory canal system. *Amia* is much better known than *Lepidosteus*, but a proper comparison of these two genera has never been made.

I propose, therefore, to describe the skeleton of *Lepidosteus*, to compare it with that of *Amia*, to discuss the systematic position of these genera, and to put forward my views as to the origin and evolution of the group to which they belong.

I have examined skeletons of *Lepidosteus platystomus*, *L. osseus*, and *L. tristoechus*; all three species are essentially similar in structure, differing from each other mainly in the shape of the bones and the number of segments of the maxillary, due to the fact that in *L. osseus* the snout is longer and narrower and in *L. tristoechus* shorter and broader than in *L. platystomus*. The nature of these differences will be seen on comparing the accompanying figures (text-fig. 1).

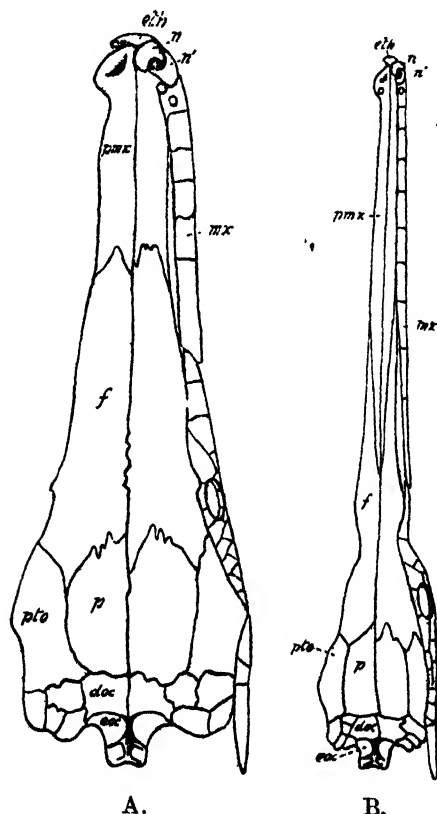
SKELETON OF *LEPIDOSTEUS PLATYSTOMUS*.

Cranium (text-fig. 2).—The skull is elongate, narrowed forward, depressed, with the upper surface flattish anteriorly and convex posteriorly. It is well ossified, but a considerable part of the otic region remains cartilaginous, and there is a large median ethmoidal cartilage running the whole length of the rostrum.

On the upper surface a transverse series of 6 dermo-occipital plates is rigidly united to the parietals, pterotics, and epiotics, and the small, simple post-temporal is very firmly attached to the dermo-occipitals, epiotic, and pterotic. Parietals, pterotics, and

frontals are normally developed. Anteriorly there is a small dermal ethmoid, and paired nasals and adnasals cover the olfactory sacs, which lie in concavities of the præmaxillaries, above the dentigerous margin of the latter. The præmaxillaries run backwards to below the frontals, expanding on the upper surface of the snout to form a pair of rugose plates (ethmo-nasals

Text-figure 1.



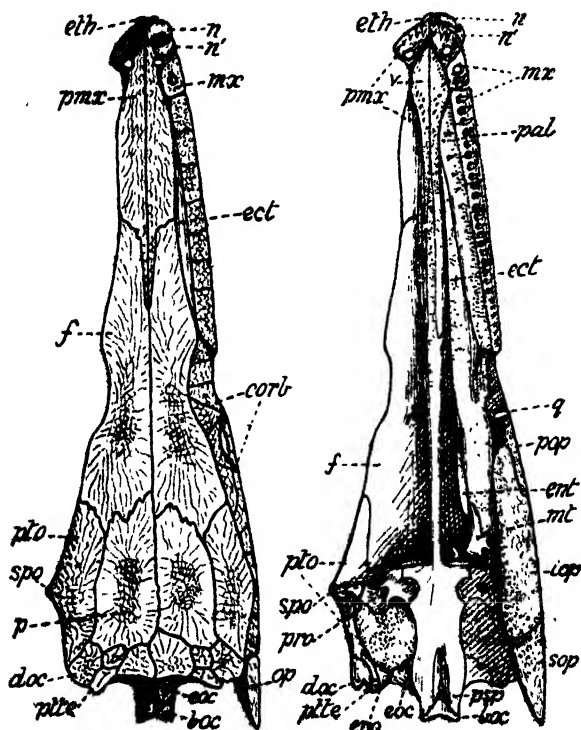
Upper surface of skull of A, *Lepidosteus tristoechus*; and B, *L. osseus*.
Lettering as in text-fig. 2.

of Parker); below this they form a pair of thick-walled tubes that carry the olfactory nerves; they embrace the slender anterior portion of the rostral cartilage and are attached below to the vomers and parasphenoid (text-fig. 3).

The vomers are laminar bones attached to the lower surface of the parasphenoid and præmaxillaries; each sends back a long,

process attached to the parasphenoid. In front of the orbital region the parasphenoid is V-shaped in transverse section, the ascending laminae overlapping the premaxillaries in front and descending laminae of the frontals behind, with the latter

Text-figure 2.



Lepidosteus platystomus. Skull from above and from below; the pterygo-quadratus, suspensorium, opercles, etc., of one side removed.

eth. mesethmoid; n. nasal; n'. adnasal; pmx. premaxillary; mx. maxillary; f. frontal; p. parietal; pto. pterotic; spo. sphenotic; epo. epiotic; pro. prootic; doc. dermo-occipital; eoc. exooccipital; boc. basiooccipital; pte. post-temporal; psp. parasphenoid; v. vomer; pal. palatine; ect. ectopterygoid; ent. entopterygoid; mt. metapterygoid; q. quadrate; corb. circumorbital; op. operculum; sop. suboperculum; fop. interoperculum; pqp. pterygo-quadratus.

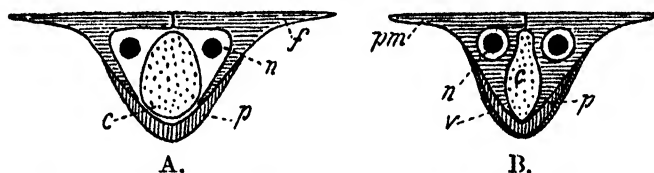
enclosing a chamber that contains the posterior part of the rostral cartilage. This does not completely fill the chamber, but on each side there is a channel for the passage of the olfactory nerves (text-fig. 3).

Behind the orbital region the parasphenoid expands, the anterior edge of each wing forming a transverse condyle for articulation with the metapterygoid. Parker's researches show that these condyles originate as separate ossifications in cartilage, and he terms them alisphenoids, but in the adult fish they are completely ankylosed with the parasphenoid.

The true alisphenoids were not seen by Parker; they are well developed and separate; they meet the pro-otics behind and are in contact with the frontals above; anteriorly they join the orbitosphenoids, which converge and ankylose anteriorly to form a short vertical plate that rests on the parasphenoid; just behind this anterior plate the orbitosphenoid is pierced on each side for the passage of the olfactory nerves (text-fig. 4).

The parasphenoid condyles are continued on to the pro-otics, which intervene between the parasphenoid and the sphenotics; inner laminae of the pro-otics meet in the middle line and form a roof for the myodome; the pterotics ossify downwards a short

Text-figure 3.



Lepidosteus platystomus. Diagrammatic transverse sections of the snout: A, at the level of the posterior end of the maxillary; B, at the middle of the length of the premaxillaries.

c. rostral cartilage; f. frontal; n. olfactory nerve; p. parasphenoid; pm. premaxillary; v. vomer.

distance in the cartilaginous wall of the otic region, and the epiotics are well developed; there are no opisthotics. The exoccipitals meet, and behind them upper wings of the basioccipital almost meet in the middle line, roofing the *foramen magnum*.

Circumorbitals, etc. (text-fig. 5, A).—The orbit is surrounded by a complete series of 12 circumorbital bones; these appear externally as flat plates, but internally they are strengthened by a stout circular ridge. There are 3 præorbitals, the anterior overlapping the end of the maxillary. Behind the circumorbitals the cheek is covered with a number of irregularly arranged plates.

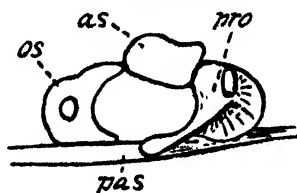
Jaws, Suspensorium, etc. (text-fig. 5).—The premaxillaries have already been described. The maxillary is segmented into 8, the anterior piece firmly fastened to the side of the premaxillary, the others attached to the palatine and ectopterygoid.

In the lower jaw the concave surface for the articulation of the convex condyle of the quadrate is formed by the posterior face of

an upper and the superior face of a lower ossification in Meckel's cartilage. There are well-developed angular and "supra-angular" bones, the latter curving in above the coronoid elevation. On the inner side there is posteriorly a large laminar præarticular, which ossifies through the coronoid cartilage below the anterior part of the supra-angular. In front of this a ridge of the dentary, parallel to its margin, is covered by two elongate dentigerous laminae, the shorter anterior one entering the symphysis, the posterior ascending the coronoid elevation for a short distance external to the præarticular; on one side a small bone is intercalated at the junction of these two bones, which may be termed intra-dentaries. The præarticular and intra-dentaries are often termed collectively "splenials," but it is very improbable that any of them is the homologue of the true splenial.

The pterygo-quadrate is completely separated from the hyoid arch, and supported by it only through the articulation of the quadrate with the præoperculum. The ectopterygoid is a very long and stout bone; anteriorly it articulates with the præmaxillary above the expanded head of the vomer; the posterior

Text-figure 4.



Lepidosteus platystomus. Orbitosphenoid (os.), alisphenoid (as.), and pro-otic (pro.) bones; pas. parasphenoid. Lateral view.

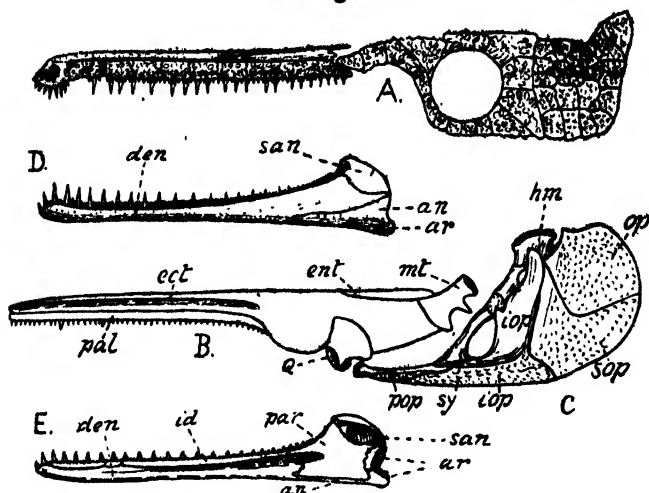
seven segments of the maxillary are firmly united to its outer face, which has a groove for their attachment; the long laminar palatine is attached to its lower surface. The entopterygoid is small, the metapterygoid bears a process for articulation with the parasphenoid and pro-otic, and the quadrate has an anterior condyle for articulation with the lower jaw and a posterior one for articulation with the anterior end of the præoperculum.

The large interoperculum is rigidly attached to the hyomandibular, symplectic, and præoperculum; the last-named is reduced to a small bone that lies above the anterior part of the interoperculum and ends in a concave facet for articulation with the quadrate. Collinge and Allis transpose the names of the præoperculum and interoperculum, on the ground that the latter is attached to the hyomandibular and transmits a branch of the sensory canal system. It may be pointed out that the interoperculum is quite normal in its relation to the suboperculum behind and the lower jaw in front, and that where it is in

contact with the præoperculum the latter lies above it. Also the analogous case of *Phractolæmus* may be quoted; in that genus the very large interoperculum transmits the sensory canal, but it is the horizontal limb of the præoperculum that is lacking, whereas in *Lepidosteus* the vertical limb has gone.

The operculum articulates with a knob on the hyomandibular, the suboperculum is well developed, and there are 3 branchiostegal rays.

Text-figure 5.



Lepidosteus platystomus.

A. Premaxillary, maxillary, circumorbital, and cheek bones.

B. Palato-quadrate (outer view).

pal. palatine; ect. ectopterygoid (showing groove for attachment of maxillary); ent. entopterygoid; mt. metapterygoid; q. quadrate.

C. Opercular bones, etc.

hm. hyomandibular; sy. symplectic; op. operculum; sop. suboperculum; iop. interoperculum; pop. præoperculum.

D, E. Lower jaw, outer and inner aspects.

den. dentary; an. angular; san. supra-angular; ar. articulars; par. præ-articular; id. intra-dentaries.

The hyoid arch comprises the hyomandibular, which articulates with the sphenotic and pterotic, the symplectic, which is firmly attached below to the præoperculum but is remote from the quadrate, the interhyal, the ceratohyal, the hypohyal, and a median basihyal. The ceratohyal has two ossifications, the hypohyal only one. The upper ossification in the ceratohyal is generally termed "epihyal;" this is certainly wrong, and I

think that there can be little doubt that the hyomandibular is the true epihyal, *i. e.* the epibranchial of the hyoid arch.

Vertebral Column.—The vertebræ are solid and opisthocœlous, with the neural arches and parapophyses ankylosed to the centra. The vertebræ number 66; from the fifty-third the vertebral column curves upwards and the vertebræ decrease in size. The neurapophyses of the first two vertebræ are short and stout; those of the succeeding vertebræ are prolonged into slender spines; the spines of each pair are in contact distally, but remain separate; the last six vertebræ have no neural spines and the last three no distinct neurapophyses. The series of supraneurals extends backwards from the first vertebra to the dorsal fin, and reappears above the end of the vertebral column, where 4 bones (epaxial supports of the caudal fin) are probably to be interpreted as belonging to it. Each supraneural is more or less expanded or even bifid proximally; the first two are short and stout, and articulate with the neurapophyses of the first two vertebræ; the rest are slender, attached to the neural spines. The ribs are expanded proximally for articulation with the distal ends of the strong transverse parapophyses. From the forty-first vertebra backwards the parapophyses become shorter and are directed downwards; their ribs also are downwardly directed, and behind the anal fin unite to form hæmal spines; the hæmal spines of the upturned vertebræ are expanded as hypurals to support the caudal fin; the hypurals are only one less in number than the upturned vertebræ, but in the specimen examined they are displaced, so that the sixtieth vertebra bears two and some of the last six vertebræ do not bear any.

Fin Skeleton.—The dorsal and anal fins are supported by a series of pterygiophores, each of which is divided into a long proximal (basal) and a short distal (radial) segment; each fin-ray is articulated to its radial. The pelvic bones are rather long and flat; they converge and slightly overlap anteriorly; only the innermost radial is well developed, the fin-rays articulating directly with the pelvic bones. The pectoral arch includes a small simple post-temporal, which is firmly united to the skull, a supra-cleithrum, and a cleithrum. The coracoid cartilage has only one ossification, the hypercoracoid (or "scapula"); there are 4 radials, 3 of which articulate with the hypercoracoid and one with the metapterygium.

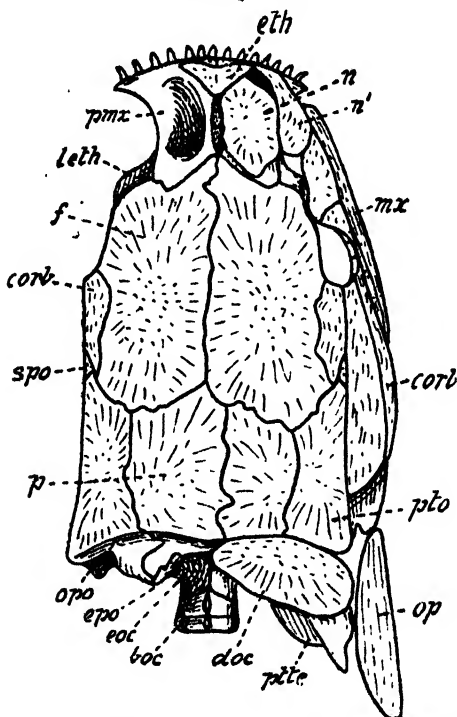
COMPARISON OF *LEPIDOSTEUS* WITH *AMIA*.

Cranium.—In *Amia* the orbito-rostral part of the skull is much shorter and broader than in *Lepidosteus*, and the *cavum cranii* extends forward between the orbits to the ethmoid region. On the upper surface a single pair of loose dermo-occipital plates represent the three pairs or more of *Lepidosteus*; the other bones, parietals, pterotics, frontals, premaxillaries, nasals, adnasals, and dermal ethmoid, have precisely the same relationship to each

other as in *Lepidosteus*, differing only in form and proportions; owing to the shortness of the snout the præmaxillaries are scarcely exposed on the upper surface behind the nasals, and when the nasals and adnasals are removed it is seen that the long tubes that carry the olfactory nerves in *Lepidosteus* are represented by mere foramina.

The rostral cartilage contains paired septo-maxillary and lateral ethmoid ossifications; the vomers and parasphenoid are broad and flat, and the latter is unconnected with the frontals; the

Text-figure 6.



Amia calva. Skull from above. For comparison with text-fig. 2.
Lettering as before.

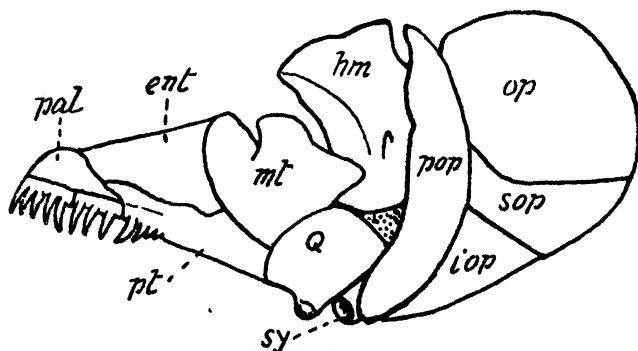
wings of the parasphenoid do not bear condyles and do not unite with the pro-otics, but extend upwards to unite by suture with the sphenotics and internally with the alisphenoids; the orbito-sphenoids are paired and separate. Small paired basisphenoids are present, narrowly separated and projecting upwards in front of the pro-otics, which roof the myodome just as in *Lepidosteus*; sphenotics and epiotics are much as in *Lepidosteus*, but in addition there are well-developed opisthotics, and above them on

each side a posterior temporal fossa roofed by the epiotic and pterotic. Exoccipitals are as in *Lepidosteus*, but the upper wings of the basioccipital in that genus are represented in *Amia* by two or three pairs of bones, generally interpreted as the neural arches of centra incorporated in the basioccipital.

Circumorbitals.—In *Amia* the circumorbital series is incomplete above, and the bones are reduced in number; there is a single præorbital, two large postorbitals cover the cheek, and above them a smaller one appears at the side of the frontal as a bone of the cranial roof.

Jaws, Suspensorium, etc.—As already noted, the præmaxillaries of *Amia* have the same relation to the dermal ethmoid, nasals, adnasals and frontals, and to the olfactory sacs and nerves as in *Lepidosteus*, but the maxillaries are quite unlike those of that genus, for they are unsegmented and free; each has an inwardly

Text-figure 7.

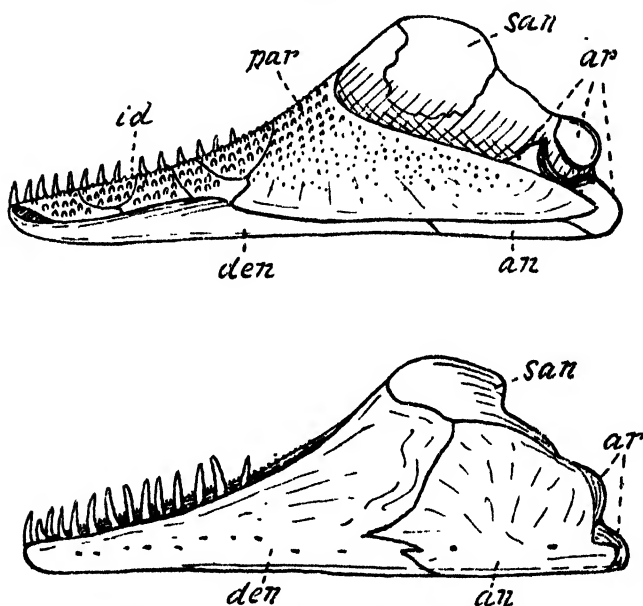


Amia calva. Pterygo-quadrates, suspensorial, and opercular bones.
Lettering as in text-fig. 5.

directed articular process at the anterior end, and each carries a supplemental bone (or supramaxillary). The lower jaw of *Amia* has two endosteal bones for articulation with the quadrate as in *Lepidosteus*, but there is an additional small bone in front of the upper of these, and above them is another additional bone with a convex posterior surface for articulation with the concave anterior end of the symplectic. The dentary, angular, and supra-angular correspond to those bones in *Lepidosteus*, and, as in that genus, there is a large laminar præarticular; in front of this Allis shows two intra-dentaries, but in the skeleton I have examined, the posterior of these is represented on one side by four bones and on the other by six; also in my example the endosteal mento-Meckelian figured by Allis appears to be fused with the anterior intra-dentary.

Except that the palatine is separable into an endosteal ossification and two dentigerous laminae, the pterygo-quadrate, hyoid, and opercular bones are the same as those of *Lepidosteus*; but they are very differently arranged, for the metapterygoid is firmly attached to the hyomandibular and the quadrate to the symplectic, the well-developed crescentic præoperculum is united to the hyomandibular and symplectic, and the interoperculum is normally developed and movable. Some authors have described a process of the metapterygoid as articulating with the prootic, but actually there is no such articulation, and the process,

Text-figure 8.

*Amia calva*. Lower jaw, inner and outer aspects.

Lettering as in text-fig. 5.

which is an intermuscular lamina directed upwards, forwards, and outwards, does not go anywhere near the otic region of the skull.

Amia has a good series of branchiostegal rays and a median gular plate. The ceratohyal has two ossifications and the hypohyal one as in *Lepidosteus*, and the branchial skeleton shows no important differences from that genus.

Vertebrae and fins.—The vertebral column of *Amia* is well known; the most important differences from *Lepidosteus* are that the vertebrae are amphiœelous, and that in most of the

caudal vertebræ each centrum is divided into a præcentrum (without arches) and a postcentrum. The terminal vertebræ, hypurals, etc., are arranged much as in *Lepidosteus*. The skeleton of the fins is as in *Lepidosteus*, except that the pectoral radials are more numerous and more than one articulates with the metapterygium; the pectoral arch differs from that of *Lepidosteus* in that the coracoid cartilage is unossified and the post-temporal is large and loosely attached, with a lower fork running to the opisthotic.

Systematic Position of *Lepidosteus* and *Amia*.

It is probable that most of the characters in which *Lepidosteus* and *Amia* agree are common to all the Holostean Ganoids (Semionotidæ, Pycnodontidæ*, Macrosemiidæ, Eugnathidæ, Amiidæ, Pachycormidæ†, Aspidorhynchidæ). Further, it is evident that the essential features which distinguish *Lepidosteus* from *Amia*, i. e. the characters of the jaws, suspensorium, and opercles, distinguish it also from all the others. *Lepidotus* is extremely like *Amia* in its head skeleton, except that the skull is more compressed, with the epiotics meeting above the exoccipitals and the orbitosphenoids united (cf. Smith Woodward, P. Z. S. 1893, and Mon. Palæontogr. Soc. 1916-1919). I am fairly certain that I can make out in this genus the symplectic articulation with the lower jaw.

The Semionotidæ, to which family *Lepidotus* belongs, first made their appearance in the Upper Permian, and are very distinct in structure from the Palæoniscidæ, the only fishes known which can be regarded as their ancestors. The typical Palæoniscids appear to have been swift-swimming predacious fishes, with a large mouth and sharp teeth. If we regard them as giving rise to the Semionotidæ, probably slow-swimming bottom-feeding fishes, with a small mouth and styliform or tritoral teeth, we can interpret many of the differences as related to a change of habits.

The change from dorsal and anal fins with numerous rays forming a close-set series to fins with the rays relatively few and spaced, each ray with its own pterygiophore, and the reduction of the muscular lobe at the base of each fin and of the radial segments of the pterygiophores, are readily understandable if the use of these fins changed from cleaving the water and withstanding strains to performing the delicate movements of a fish at rest or swimming slowly. Correlated with this modification of the dorsal and anal fins is that of the caudal, the upturned end of the

* These are aberrant in the reduction of the opercular apparatus and the arrangement of the bones of the cranial roof.

† The præmaxillaries are said to be loose and separated by an ethmoidal rostrum, but I am not satisfied that this interpretation is correct. I think that the so-called præmaxillaries may be the fractured anterior ends of the maxillaries.

tail being shortened so that the fin became terminal rather than ventral. The use of the jaws for crushing shell-fish instead of seizing fishes may account for the firm union of the præmaxillaries with the frontals. The lower jaw of the Palæoniscids appears to have consisted of the same four bones as that of *Polypterus*, namely dentary, angular, articular, and præarticular; that of the Semionotids is shorter, deeper, and stronger, and the additional articular ossifications (as seen in *Amia*) may simply be due to the increased size and complexity of its articulation, whilst the intra-dentaries may be regarded merely as plates developed to support teeth. The "supra-angular" may be an anterior bone of the outer circumorbital series which has adhered to the coronoid process, in the same way that a bone of the temporal series has become attached to the hyomandibular in *Polypterus*; and I believe that the supplemental maxillary had a similar origin. The small size of the mouth involved a change in shape and direction of the præoperculum and hyomandibular; the præoperculum, which in the Palæoniscidæ appears to have been simply a plate covering the cheek behind the circumorbitals, now became used to strengthen the suspensorium, a necessity on account of the forward position of the articulation of the lower jaw; the lower end of the elongated hyomandibular ossified as the symplectic, which may have been originally developed either, as I am inclined to think, for the articulation of the lower jaw, or perhaps only to support the quadrate and connect it with the præoperculum; the original hyomandibular ossification developed a knob for articulation with the operculum; the upper ossification in the cerato-hyal appears to have been developed for the attachment of the interhyal, which seems to be an ossified ligament. It is obvious that the character of the respiration would be greatly changed, the movements being smaller, and I think that a better regulation of these would result from the definite articulation of the operculum with the hyomandibular; moreover, the hyomandibular being now but little movable, movements of the operculum became of more importance. The interoperculum is a new bone of some interest; it would almost seem as if the suboperculum, retaining its attachment to the posterior end of the lower jaw, had been elongated and then fractured, the posterior part thus retaining its freedom of movement, whilst the anterior—the interoperculum—was overlapped by the horizontal limb of the præoperculum. Finally, one may suspect that the disappearance of the clavicles is in some way connected with the other readjustments in this region.

The Semionotidæ appear to have developed in various directions, giving rise for example to the remarkable Pycnodontidæ, which show many resemblances to our modern Plectognaths; and through the Eugnathidæ to the Amiidæ and to the Pachycormidæ, which parallel the Scombroids. The development of a large-mouthed piscivorous type appears to have taken place in two

ways. In the Eugnathidæ the cleft of the mouth extended backwards and the suspensorium became vertical or directed backwards; in these strong-swimming fishes the dorsal and anal rays have increased in number and become concentrated, and the caudal has become forked. On the other hand, in the Lepidosteidæ the snout and lower jaw have grown forward, the quadrate retaining its anterior position, and we may suppose that as the lower jaw became longer and more powerful the strain on the suspensorium was relieved by the acquirement of the articulation of the metapterygoid with the parasphenoid. Other modifications, such as the great development of the interoperculum, seem to be related to the elongation of the orbital region, which gives an increased surface for attachment of the strong mandibular muscles. In these sluggish, lurking fishes the fins remain essentially as in the Semionotidæ.

The Aspidorhynchidæ, which have sometimes been associated with the Lepidosteidæ, have none of the peculiarities of that family. An analysis of their characters shows a close agreement with the Eugnathidæ, from which they differ in the prolongation of the præmaxillaries to form a beak and the development of a præsymphyseal bone in the lower jaw. Especially important is the resemblance of the symplectic to that of the Eugnathidæ and *Amia* (Smith Woodward, Monogr. Palæont. Soc. 1916-1919, p. 98, pl. xx. fig. 2).

It is well known that the Teleostean agree with the Holostean Ganoids in the structure of the dorsal and anal fins, the absence of clavicles (infra-clavicles), and the structure of the suspensorium and opercles. But the most primitive Teleosteans (*e. g.* the Elopidae) differ from the Holostei in several important respects, as follows:—The caudal fin is homocercal*. There are three coracoid bones (hyper-, hypo-, and meso-coracoid), whereas in *Lepidosteus* and *Amia* there is not more than one (hypercoracoid or "scapula") and the mesocoracoid bridge is cartilaginous. The pectoral radials are all inserted on the hypercoracoid and hypocoracoid, the lowest radial probably representing the metapterygium. An endochondral supraoccipital bone is present. The vomer is unpaired. The lower jaw has no "supra-angular" and no intra-dentaries, and the præarticular is reduced†. The præmaxillaries are loosely attached, remote from the frontals, and in front of the olfactory sacs.

* Regan, Ann. Mag. Nat. Hist. (8) v. 1910, p. 353.

† The current nomenclature of the Teleostean lower jaw is faulty. The bone usually called angular is the homologue of the lower articular of *Amia* and the single articular of *Polypterus*. Ridewood's "endosteal articular" is the homologue of the upper articular that articulates with the quadrate in *Lepidosteus* and *Amia*. His "ectosteal articular" is the angular, and his "sesamoid articular" in all probability the præarticular.

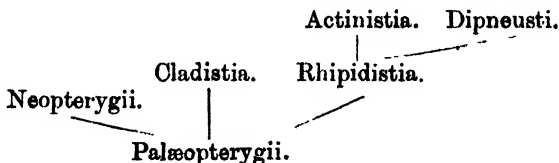
According to Ridewood (P. Z. S. 1904) the bone last named serves for the attachment of the tendon of part of the levator muscle, but it may well have persisted rather than have been developed for this purpose. In the Cyprinodonts the opisthotic is reduced to a nodule to which the lower fork of the post-temporal is attached.

If only the living forms were considered, it might be held that the Chondrostei, Holostei, and Teleostei were groups of equivalent rank. But a study of the fossils shows that this conclusion is wrong. The mesozoic Pholidophoridæ and Oligopleuridæ resemble the Holostei in the structure of the caudal fin (and in the Pholidophoridæ of their scales), but in other characters, such as the small loose præmaxillaries, the maxillary with convex oral edge and bearing two supramaxillaries*, and the absence of a "supra-angular," they show clear evidence of their relationship to the Elopidae.

The Pholidophoridæ had minute teeth, and were probably plankton-feeders like the Herrings, which they resemble in form and in the shape of the fins. They are evidently another offshoot of the Semionotidæ, from which they differ especially in the structure of the mouth, and they lead to the Leptolepidæ and Elopidae. These are stronger swimmers, with a deeply-forked caudal fin, in which the upper hypurals are for the first time supported by uroneurals, paired bones that replace the upturned end of the vertebral column.

The Holostei and Teleostei, therefore, are one group, for which it seems better to use the name Neopterygii, rather than to use Holostei or Teleostei in a new and extended sense; whilst the name Palæopterygii may be used to designate the group including the Palæoniscoids, Chondrostei, and Belonorrhynchi.

I have long considered that the Selachians constitute a distinct class (cf. P. Z. S. 1906, p. 724), and if that be admitted, the main groups of the Pisces† may be termed subclasses. These are six in number—namely Palæopterygii, Neopterygii, Cladistia, Rhipidistia, Actinistia, and Dipneusti, the probable relationships of which are indicated in the following scheme:—



The Neopterygii are defined by the dorsal and anal fins with pterygiophores equal in number to the dermal rays, the absence of clavicles and of paired gulars, the presence of an interoperculum,

* It is worth noting that one supramaxillary and a supra-angular, and two supra-maxillaries and no supra-angular are alternative conditions, almost suggesting that the maxillary has captured the supra-angular from the lower jaw. But it seems more likely that the supra-angular has gone, and that as the maxillary lengthened another suborbital has become attached to it.

† I exclude from the Pisces a number of Palæozoic groups of uncertain relationships, e. g. Arthrodira, Asterolepida, Osteostraci, etc.

and by the structure of the skull (e.g. typically 5 otic bones, alisphenoids and orbitosphenoids, etc.) and of the hyoid arch (a symplectic, two ossifications in the ceratohyal, etc.). This subclass contains the great majority of living fishes, and includes a large number of orders, of which the first three are :—

Order 1. PROTOSPONDYLI.

Caudal fin abbreviate heterocercal. Vertebral column acentrous, or with centra variously developed*. Præmaxillaries fixed, attached to frontals and pierced for passage of olfactory nerves; maxillary free, unsegmented, usually with a supramaxillary. Lower jaw with "supra-angular," large dentigerous præarticular, and intra-dentaries. Hyoid arch and præoperculum normally developed, and symplectic firmly attached to quadrate. Only one coracoid ossification, or none; mesocoracoid bridge cartilaginous; one or more pectoral radials inserted on metapterygium.

Principal families :—Semionotidæ, Macrosemiidæ, Eugnathidæ, Amiidæ, Pachycormidæ, Aspidorhynchidæ, Pycnodontidæ.

Order 2. GINGLYMODI.

Distinguished from the preceding by the characters of the jaws, suspensorium, and opercles. Maxillary segmented, the first one or two segments attached to præmaxillary, the rest to ectopterygoid; metapterygoids articulating with transverse facets on wings of parasphenoid; hyoid arch free from pterygo-quadrate; præoperculum small, its anterior end articulating with a condyle on quadrate; interoperculum large, fixed, connecting hyomandibular with præoperculum. Vertebral centra solid, opisthocœlous.

One family, Lepidosteidæ.

Order 3. HALECOSTOMI.

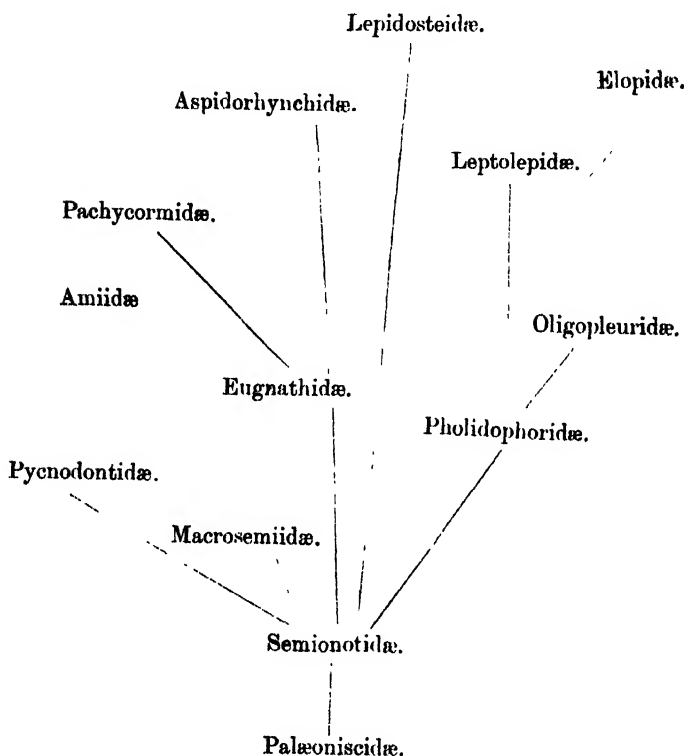
Caudal fin abbreviate heterocercal. Præmaxillaries small, loosely attached; maxillary typically with two supramaxillaries; lower jaw without "supra-angular" or intra-dentaries. Vertebral centra annular or amphicœlous.

Two families, Pholidophoridæ and Oligopleuridæ.

* The various conditions are :—(1) No centra; bases of arches not expanded. (This is found in all families except Amiidæ and Aspidorhynchidæ.) (2) No centra; bases of arches may form laminar expansions over the notochord (some Pycnodonts). (3) Annular or amphicœlous centra of uncertain origin; no præ- and post-centra (Aspidorhynchidæ, *Neorhombolepis*). (4) Solid outgrowths of arches may enclose notochord, forming annular centra, with præ- and post-centra in caudal region. (Some Macrosemiidæ, Eugnathidæ, and Pachycormidæ.) (5) Centra disc-like, formed by ossification of tissues surrounding notochord, enclosing bases of arches; præ- and post-centra in caudal region (Amiidæ).

The fourth Order, the *ISOSPONDYLI*, is distinguished from the *Halecostomi* by the homocercal structure of the caudal fin; it is followed by the Orders *OSTARIOPHYSI*, *APODES*, etc.

The relationships of the families dealt with above may be expressed diagrammatically as follows:—



GENERAL CONSIDERATIONS.

In dealing with the origin and evolution of the lower Neopterygian Fishes I have tried to emphasize the conclusion at which I have arrived, that their differentiation has been adaptative, changes of structure being especially related to the nature of the food and the method of procuring it.

This is well illustrated by the following example:—The Semionotidæ, probably slow-swimming fishes feeding on molluscs, crustaceans, etc., appear to have been derived from the Palæoniscidæ and have themselves given rise to the Eugnathidæ,

which resemble the Palæoniscidæ in form, shape of the fins, size of the mouth, and structure of the teeth.

In comparing *Eugnathus* with *Palæoniscus*, both strong-swimming predacious fishes, it is not evident that any of the differences between them are adaptative. But these differences are due to the Semionotid ancestry of the Eugnathidæ, and there is good reason for believing that they were adaptative in origin.

The later evolution of the Neopterygian Fishes offers numbers of parallel examples; modifications persist and become the basis for further modifications.

25. On the Origin of Flight in Birds.

By Baron FRANCIS NOFCSA.

[Received April 24, 1923: Read April 24, 1923.]

(Text-figures 1-7.)

In 1907 I brought forward the idea that birds originated from bipedal Dinosaur-like running reptiles in which the anterior extremities, on account of flapping movements, had gradually turned to wings without thereby affecting terrestrial locomotion (14). This idea has been on several occasions criticised by various authors (1, 3, 9, 12, 16).

In consequence of new material having turned up that has some bearing on this subject, the time seems to have arrived when the different criticisms to which the hypothesis of a "running *Proavis*" has been subjected can be reviewed.

The first criticism was brought forward by Hay (9), who disagreed with my idea on account of my having drawn *Proavis* with too short arms and with a reduced and rotated hallux. According to Hay's view, birds never could have originated from such a form unless considerable rejuvenation might be presumed. The Dinosaurs Hay supposes to have been originally quadrupedal.

Hay's view was endorsed by Abel (1), who, on account of the rotation of the hallux and the development of a prehensile manus in *Archæopteryx* and Dinosaurs, in 1912 supported the idea that both birds and Dinosaurs were derived from arboreal forms. Steiner tried to derive arguments against my hypothesis from the diastaxic arrangement of the feathers, the origin of which he traced back to some arboreal Agamid (16). In a later paper (17) he likewise emphasised the prehensile structure of the manus in primitive birds, but at the same time he believed that Abel's arguments, based on hallux and pollex, were devoid of foundation.

Beebe (3) and Lucas (12) fully appreciate the difficulty that arises from the fact that, while in all arboricolous passive fliers the centre of the parachute surface coincides, as it must, with the centre of gravity of the animal, this could not have been the case in a primitive arboricolous bird having feathers only on its tail and arms. They think to overcome this difficulty by assuming that the most primitive arboreal birds had quills also on their legs.

This stage in avian evolution Beebe terms the *Tetrapteryx* stage; and in support of his hypothesis, he falls back on the observation that temporarily quills develop on the legs of several kinds of birds, and are later replaced by down.

In 1922 Abel (2) dropped the idea that birds and Dinosaurs originated from quadrupedal arboreal forms, and suggested that birds might be the offspring of a bipedal *Tarsius*-shaped reptile. Heilman tried (11) to reconcile my views with those held by Hay and Abel, etc.

It is apparent from this review, that anatomical arguments against the hypothesis of a running *Proavis* are mainly based on the structure of the manus and the pes, and partly on the occurrence of certain quills. None of the authors cited has considered either the shoulder-girdle or the pelvis of birds, in spite of these parts being correlated with the feet.

Since Hay and Abel's argument from the occurrence of a functional hallux in different birds is of great anatomical weight, it has to be dealt with first. The functional hallux in many birds must either be an old structure inherited from an arboreal *Proavis*, or it must be a newly-acquired character that was missing in the running *Proavis*.

Although we know comparatively little about the Triassic bipedal reptiles among which the running *Proavis* might be looked for, nevertheless by the study of fossil footprints some points of the structure of the feet of bipedal Triassic reptiles can be elucidated (13). In my argument, four types of Triassic footprints are of special interest, for they throw some light on the evolution of the hallux in these otherwise nearly unknown types. These four types can be grouped around the footprints called *Plectoterna*, *Ammopus*, *Anchisauripus*, and *Gigandipus*. Believing that I have proved all Dinosaurs to have developed from bipedal lightly-built animals (15), I consider these tracks to be Dinosaurian.

Plectoterna has long and slender toes, and a very long metatarsus resting always on the ground and indicating a plantigrade animal like *Hallopus* (text-fig. 1). *Ammopus* has also slender toes, but it shows, instead of the metatarsal impression only, the impression of a rounded pad, proving that this animal was digitigrade, as is *Procompsognathus* (text-fig. 2). *Anchisauripus* has thicker toes than either of these two types, and was frequently plantigrade. It is the track of *Anchisaurus* (10) (text-fig. 3). *Gigandipus* is of still heavier build, but always digitigrade, and the track of some unknown Megalosaurian.

Around each of these four types several other Triassic footprints can be grouped that differ mainly in the development of the hallux. To the *Plectoterna* type belong *Palamopus*, *Exocampe*, *Herpedactylus*, *Xiphopeza*, and *Corvipes*; to the *Ammopus* type are allied *Eupalamopus*, *Polemarchus*, and *Platypterna*; the *Anchisauripus* type is suggested by *Anomæpus*, *Apatichnus*, and *Grallator*; and the *Gigandipus* type is approached by *Sauropus* and *Hyphepus*.

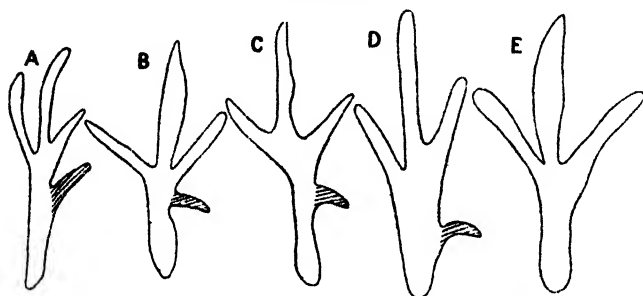
Considering the hallux of these different tracks, it may be remarked that in some the hallux articulates very low down and is not rotated (*Palamopus*, *Exocampe*, *Anomæpus*); in others the

rotation is more or less marked, but the hallux is still always well in touch with the ground (*Herpedactylus*, *Xiphopeza*, *Platypterna*, *Palamopus*, *Polemarchus*); yet in other tracks (*Ammopus*, *Apatichnus*, *Anchisauripus*, *Sauropus*) the rotation is still more accentuated, and the articulation is well raised above the ground, so that only the tip of the hallux makes an impression; and finally in some of the tracks (*Corvipes*, *Platypterna*, *Grallator*) the hallux can be seen no more.

Thus in all four types of tracks a simultaneous and independently acquired rotation and abbreviation of the hallux can be detected. Since it is quite impossible to assume that all four types of tracks were exclusively made by animals becoming arboreal, it is evident that the curious rotation of the hallux in all these types was not due to arboreal adaptation, but to some other hitherto unknown factor*.

The hallux that is attained in all these types recalls that

Text-figure 1.



Footprints of plantigrade Triassic reptiles.

(A) *Herpedactylus*; (B) *Xiphopeza*; (C) *Plectopterna*; (D) *Plectopterna*;
(E) *Corvipes*.

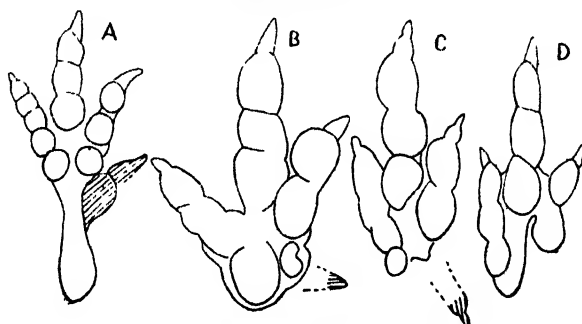
of those birds in which it is a non-functioning digit. If it can be proved that the functioning hallux in birds developed from a non-functioning hallux, this observation is a strong argument for a Dinosaur-like terrestrial bipedal running *Proavis*.

If the functioning hallux in birds developed from a non-functioning but rotated and abbreviated hallux, this change must have left some traces. In the functioning hallux of birds two distinct features seem actually to point to such a change. First, one may mention that even in birds with a strong functioning hallux the first metatarsal is reduced. This shows that in the history of these birds some stage of evolution was passed in which the hallux was but feebly attached to the leg, and when consequently the hallux was not much used for grasping.

* The reason why the rotated hallux is more reduced in some Dinosaurs than in others will be discussed on another occasion.

As a second feature pointing in the same direction, the great variety of the flexor muscles of the hallux can be brought forward. If the functioning type of hallux were the primitive type in birds, then the arrangement of the flexor muscles could be everywhere alike, whereas, if the hallux was rejuvenated and secondarily but independently strengthened in different groups of birds, the flexor muscles might vary. As is known, the latter is actually the case, and the variation has been used in the classification of birds (7). These detailed observations show that the functioning hallux in birds is perhaps a secondary adaptation. A feature worth mentioning is that in the apparently tridactyle foot of those bipedal animals that passed through a stage of arboreal specialisation (Kangaroo) the fourth toe is the longest (5), while it is the third that is the longest in Dinosaurs, birds, and *Alactaga* (14).

Text-figure 2.



Footprints of digitigrade Triassic reptiles.

(A) *Anomacopus*; (B) *Apatichnus*; (C) *Anchisauripus*; (D) *Grallator*.

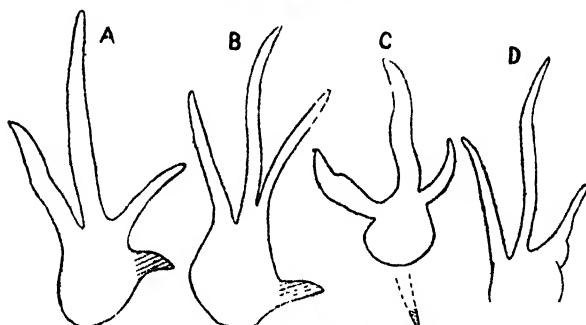
Turning now from the pes to the manus in primitive birds (*Archæopteryx*), it may be remarked that this is a long and slender organ, adapted to some extent for grasping, but this alone is again no sign of arboreal specialisation.

The partial use of the anterior limb as a grasping organ occurs in different terrestrial quadrupeds. The fore leg is used as a manus in the Kangaroo when taking up food; it is similarly used in mice and rabbits and, partly for the same purpose and partly also as a weapon, in cats and bears. Members of each of these groups are, it is true, partly also arboreal; but nevertheless the terrestrial representatives in these groups do not descend from the arboreal forms, for, on the contrary, it was the use of the anterior limb as a grasping organ that enabled some of the terrestrial forms to climb trees.

Steiner has proved in a recent highly valuable contribution (17)

that in most *Archosauria* the ulnar phalanges are reduced, while the radial phalanges are retained or sometimes even strengthened. He takes this to be a sign of the arboreal adaptation of *Proavis*. The reduction cannot be denied, but again it does not seem to be a sign of any arboreal specialisation. In the one group of extinct reptiles that certainly was derived from arboreal types this reduction does not take place, for in Pterosaurians the last finger is very strong, and this reduction does not occur in any of the arboreal mammals (5). It is well marked only in Crocodilia, Dinosaurs, and birds. The primitive Dinosaurs are, as is well known, bipedal (15). In the Crocodilia the reduction of the shoulder-girdle and the curious elongation of the carpal bones indicate that formerly also in this group the disproportion between the fore limbs and the hind limbs was also decidedly greater (10). Considering that all those mammals that are partly bipedal use the anterior limb for

Text-figure 3.



Footprints of digitigrade Triassic reptiles.

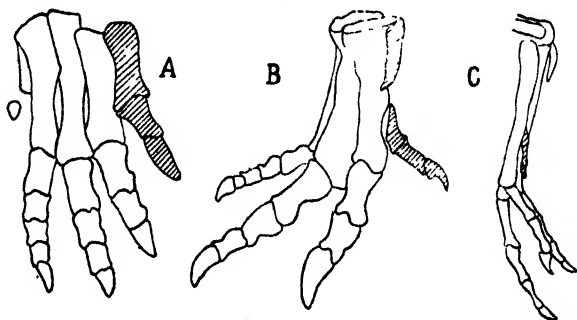
- (A) *Eupalamopus* (somewhat modified); (B) *Polemarchus*; (C) *Ammopus*;
(D) *Platypterna*.

grasping, and that Dinosaurs and Crocodilia are terrestrial forms with a strong posterior body, it should be investigated whether the ulnar reduction is not due to the use of the manus as a grasping organ during terrestrial and not during arboreal life. The first change that is attained when both the as yet unmodified anterior limbs are used together as a primitive grasping organ, is the inward rotation of both palmar surfaces; the next change that must be expected is a strengthening of the radial side, for in two palms that are half-way rotated the radial borders of the hands come always nearer together than the ulnar borders; consequently they are always exposed to much greater strain than the ulnar sides of the hands. This greater strain will be especially felt when the food is held with both anterior feet and pieces are detached with the teeth. Such a manus must of course differ strongly from the manus of every arboreal type, for in the

arboreal types it is of importance that the grasping surface of the whole hand should be as great as possible. This is attained by the retention of all phalanges, and especially by the retention of the fourth (5). In animals in which the function of the manus is different, a reduction of the ulnar phalanges, recalling somewhat the reduction of the fourth and fifth digits of the human hand, can take place.

The most reduced manus of this sort attained by a terrestrial animal is the manus of *Struthiomimus*, and the resemblance to the manus in *Archæopteryx* is quite easily made out (18). *Struthiomimus*, however, did not live on trees (text-fig. 5). This genus is not only suitable for demonstrating that a hand can be developed on *terra firma*, but also that a secondary elongation of the fore limb can be attained without adaptation to flight (18). Comparing the Triassic *Procompsognathus*, the Jurassic *Ornitholestes*, and the Cretaceous *Struthiomimus*, none of which were arboreal,

Text-figure 4.



Bones of pes in Dinosaurs.

(A) *Massospondylus*; (B) *Antrodromus*; (C) *Compsognathus*.

it may be remarked that the anterior limb is short in *Procompsognathus*, longer in *Ornitholestes*, and longest in *Struthiomimus*. This shows a steady increase in length. Since a similar elongation occurs also in the Sauropoda (for in this group the long-armed Brachiosauridae certainly descended from the other, but short-armed forms) this elongation may well be compared with the elongation that can be seen in the anterior limb of the most primitive bird (*Archæopteryx*). It is a sort of rejuvenation that suggests also the rejuvenation of the avian hallux already discussed. This observation proves to a certain extent that Hay's objection to my drawing *Proavis* with relatively short arms does not weigh as much as it seems to do at first.

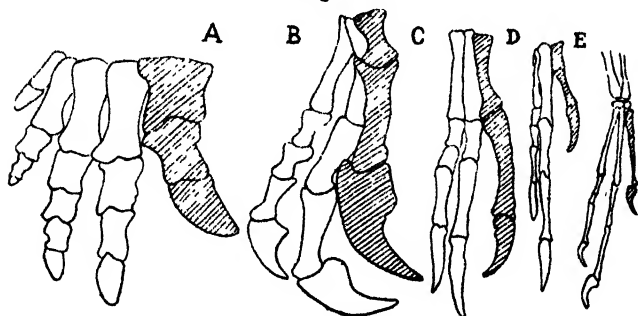
After having discovered in the course of our investigation that the similarity of hands and feet in birds and Dinosaurs, and their fundamental difference from these parts in all arboreal

mammals and lizards, not only do not form an argument for the arboreal origin of birds and Dinosaurs but on the contrary plead for their origin from running ancestors, and after having, as I believe, refuted the arguments brought forward by Abel, Hay, and Steiner, I think the next step should be to mention all those points in the anatomy of birds which exclude an arboreal *Proavis* from the history of this group.

All birds have a fused metatarsal. Where it is but feebly fused, as in the Penguins, this is a return to a primitive stage, for in the fossil Penguins of the Seymour Islands the metatarsals are more strongly fused than in any recent species (20).

With exception of arboreal birds, not a single arboreal vertebrate animal is known in which a fusion of the metatarsals is even indicated. This fusion shows that *Proavis* must have moved differently from all recent and fossil arboreal forms.

Text-figure 5.



Bones of manus in Dinosaurs and birds.

- (A) *Massospondylus*; (B) *Antrodromus*; (C) *Struthiomimus*; (D) *Ornitholestes*;
(E) *Archæopteryx*.

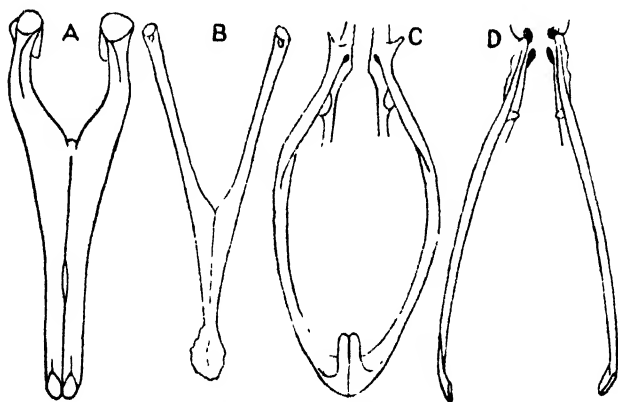
Proavis cannot have leaped in a more or less frog-like manner like *Tarsius*, *Galago*, or frogs, for in such arboreal animals the flexible tarsus is modified and its proximal part elongated; it cannot have climbed, for the manus is specialised on other lines: it cannot have jumped like a monkey, for birds show no tuber on the heel. Even *Pedetes*, though terrestrial and provided with compact tarsal bones, shows how even the firmly united tarsal bones are finally affected by jumping, for in the recent *Pedetes* these bones are somewhat elongated, while they are short in a more primitive fossil type that Prof. Stromer intends to describe. This elongation of the tarsal bones is necessary in jumping animals, for in these it is essential that that part of the pes should be rigid and long which immediately touches the tibia, and not the part beyond the flexible tarsal bones. In bipedal stalking and walking animals the metatarsals can more easily elongate so as to ensure a greater stride.

Since the fusion of the metatarsals occurs exclusively in terrestrial forms (*Alactaga*, etc., and *Artiodactyla*), *Proavis* must once have been terrestrial. Supposing *Proavis* acquired this marked specialisation while living in trees, it must have moved about there in a hitherto unknown fashion; supposing, however, that birds learnt to fly, and only then became bipedal, then we have a quite unique sort of evolution, for all those quadrupeds that learnt to fly in the quadrupedal state became unable to walk. Consequently birds must first have been bipedal, and only then have learnt to glide.

Another argument that can also be brought forward against the hypothesis of an arboreal *Proavis* can be deduced from the pelvis of the most primitive bird we know (*Archæopteryx*).

While the pes in *Archæopteryx* shows that this type had

Text-figure 6.



Pubes of Dinosaurs and birds.

(A) *Coelurus*; (B) *Archæopteryx*; (C) *Struthio*; (D) *Dromæus*.

already taken to arboreal life, the pelvis, as shown by the pubes, is of the long and narrow type. This type is only met with in Dinosaurs and one cursorial bird. In the other birds, and especially in the arboreal birds, the pelvis is usually broad and short, and the pubes are wide apart (text-fig. 6).

In accordance with this structure and with the abbreviation of the vertebral column, the arboreal birds mostly hop, while the ground birds walk or run. In the best runners the body is the longest, and the pelvis always remarkably narrow. Since a long body and narrow pelvis are seen in *Archæopteryx* in a marked manner, its arboreal specialisation can only be called very slight. It was assuredly derived from a terrestrial stock.

The shoulder-girdle in birds also indicates that their common ancestor must have once passed through a terrestrial :

specialisation. Whenever in nearly-related Mammalia terrestrial and arboreal forms occur, it is in the latter that the clavicles are certainly present. According to Weber (19), the clavicles are missing in the terrestrial genus *Hystrix*, but present in the arboreal *Erethizon*.

Since in cursorial forms in which the humerus moves only in a plane that runs parallel to the body, no lateral strain is brought to bear on the glenoidal fossa, of course in such forms clavicles are useless, but they must be retained in the forms that extend the arms strongly sideways, for here such lateral strains occur.

If birds are derived from terrestrial forms in which the arms and the shoulder-girdle were temporarily reduced, it is in the shoulder-girdle that this must show.

In the Thecodontia, in which, as shown by the relative length of the fourth digit, the elbows stood yet somewhat off from the body, an interclavicle and clavicles are present; in the Crocodilia, only the interclavicle remains, but also the fourth toe is abbreviated, showing that the lateral strain on the leg was already relatively small; finally in all the Dinosaurs, as we know, clavicles and interclavicle are absent. In Dinosaurs, moreover, a well-ossified sternum is present, arising from two centres of ossification.

If we turn now from these reptiles to modern and extinct birds, we find always an osseous sternum and further on a bone that has been considered as corresponding to the clavicle of reptiles. This bone has been called the furcula, and it is this name that I adopt, for it has no phylogenetical meaning. In some birds this bone touches the sternum, in others, as *Archæopteryx*, it does not.

Not even the slightest trace of an interclavicle has ever been found in birds (6), although this bone has been eagerly sought for. The scapula and coracoid in *Archæopteryx* recall these elements in the primitive bipedal Dinosaurs and Struthious birds (text-fig. 7).

If the present arboreal birds are the direct descendants of a clavicle-bearing quadrupedal lizard-like reptile that took to climbing trees, surely a clavicle ought to be present, and perhaps even an interclavicle might be expected, for it is exactly the interclavicle that is retained both in Crocodiles and Mosasaurs when the osseous clavicles are already gone. If features exist that show that the furcula of birds is a newly-acquired bone and that both clavicles and interclavicle are gone, then this is an important argument in favour of a primitive running *Proavis*.

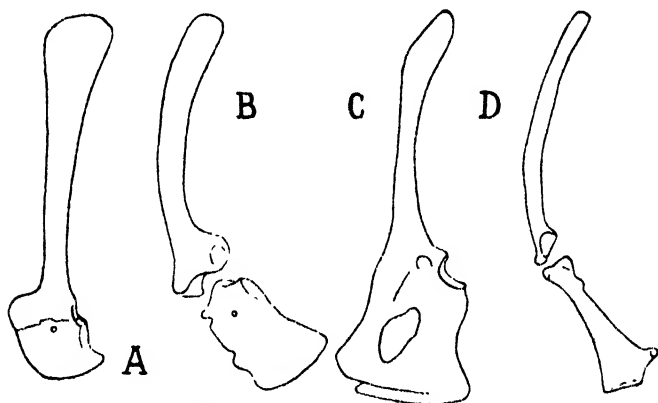
As can be seen, a great part of the question turns on the nature of the furcula of birds.

While the clavicles in all animals are always paired bones attached to the scapula with one end and to the interclavicle with the other, the furcula of birds adheres to the coracoid with one end and fuses, even in *Archæopteryx*, in the middle with the furcula from the other side.

If we wish to identify the furcula of birds with the clavicle of other vertebrata, we must assume that, first of all, the clavicle managed to slip along the anterior border of the scapula, then, to pass the glenoid fossa without, however, affecting the motion of the humerus by so doing, and finally to attach to the coracoid. Worse than that, we must also suppose that in the middle of the body a very curious, almost mysterious, and unique reduction managed to wipe out even the last ontogenetical trace of the interclavicle without affecting the clavicles. Surely it is somewhat risky to evoke a hypothesis of this sort.

Supposing now, instead of these changes, that the furcula is an ossified tendon that was developed when birds began to glide to strengthen a reduced scapular arch, it is easy to explain its origin on the coracoid, the primary fusion of the median ends, its

Text-figure 7.



Scapula and coracoid in Dinosaurs and birds.

(A) *Gorgosaurus*; (B) *Archæopteryx*; (C) *Struthio*; (D) *Nothura*.

successive fixing on to the sternum, and the absence of clavicles and interclavicle. Of course it is necessary in this case to fall back on the hypothesis of a terrestrial and bipedal *Proavis* in which the shoulder-girdle had suffered reduction.

In accordance with some old zoologists, I consider the furcula to be an ossified tendon, and not to be homologous with the clavicles in reptiles. Since this supposition agrees with the results hitherto obtained, I think this hypothesis is the right one.

All evidence brought forward up to the present shows that the flying state of birds was preceded by a state of bipedal running. Having established this, of course it becomes necessary to investigate when and where primitive feathers and passive flight began.

If passive flight and feathers arose after cursorial reptiles had

taken up an arboreal life, they must have developed feathers on arms and legs, for also in these long-necked and long-tailed forms the centre of the supporting gliding surface had to coincide with the centre of gravity of the body. Hence, evidently out of these reptiles a *Tetrapteryx* had to develop.

Of course an exclusively bipedal *Tetrapteryx* would encounter great difficulties when climbing. During gliding, furthermore, in spite of new difficulties presenting themselves, the knees of such a creature had evidently to be turned outward; the feet had to be stretched away from the body and had to be brought into the same plane as the anterior members, else the feathers of the legs would have been quite ineffective. All this and the difficulties encountered when climbing without using the anterior limbs would have been very detrimental to bipedal locomotion. Even a mere glance at Beebe's hypothetical *Tetrapteryx* shows that such a creature could not have been bipedal.

Since Beebe's *Tetrapteryx* is a rather short-necked animal, this point of his drawing is likewise open to criticism. All birds originated evidently from a bipedal and long-necked ancestor that carried the head upright. It will, however, always remain an unsolved problem how *Tetrapteryx* could have managed to carry such a long neck and an upright head when gliding: arboreal animals are rather short-necked.

In consequence of all this, the *Tetrapteryx* hypothesis, which is but a revival of Pycraft's arboreal *Proavis*, must evidently be dismissed, for it can in no way account for the persistence of bipedal locomotion in birds.

The whole *Tetrapteryx* hypothesis is based exclusively on the one interesting observation, that in some birds a row of quills is present on the upper part of the legs.

Without diminishing the interest of this observation, it has to be remarked that in a long-tailed animal this is the very place where quills would be ineffective, and that the phylogenetical value of this observation varies according to the manner in which one estimates the relation between quills and down.

If the down is considered to be the primitive type of feather which originated as a body cover to prevent the loss of heat, and the quills are considered as its modification, of course in such a case the occurrence of a row of quills on the leg can be taken as a proof that the legs were once used for flying; but if, on the other hand, the quills are considered as primitive, then such a reasoning is fallacious. In this latter case the occurrence of quills in places that are later covered with down possibly only shows that formerly a part of the side of the body of the primitive birds was covered with quills arranged in rows. Such quills can then gradually have been replaced by down, except in places where they served for flight or steering.

In such a case it may be assumed that the quills which evidently first originated on the arms and tail gradually spread to adjacent places where they were not really wanted.

A hypothesis that assumes that organs that develop in one part should be capable of spreading on to adjacent regions where they are of little or no value, needs naturally to be proved.

In all species of Rhinoceroses in which a strong nasal rugosity is present to serve as base for the dermal horns, the surface of the jugal arch, the lacrymal, prefrontal, the otic region, and even the posterior and exterior surface of the mandible, is also rough (*Rh. sumatrensis*, *Rh. bicornis*). In those Rhinoceroses, however, in which the nasal tuberosity is weak or wanting, the jugal and lacrymal and the other bones mentioned above are also smooth (*Rh. unicornis*, *Aceratherium*).

A similar feature, as in *Rhinoceros*, can be found also in Suidæ. *Hylæocherus* does not only show strong rugosities on the maxillaries and jugals, where the facial warts are developed, but also on the mandible and the frontal. *Sus verrucosus* shows similar but less marked features. Contrary to this, in *Sus barbatus* and *Sus cristatus* all the skull bones are smooth, and correspondingly on the cheeks strong warts and rugosities are wanting.

That the rapidly spreading rugosities in *Rhinoceros* and *Sus*, though in connection with warts, do not exclusively depend on the presence of these excrescences, can be demonstrated by the different Giraffes. Also in the latter a spreading of exostosis is traceable until the whole head is covered and even the mandible is affected: nevertheless, the skin in these animals remains smooth, and is quite normally covered with hair. Less clearly than in these three groups, the spreading of useless exostosis can be observed in the bovine tribe. In *Bos bubalis*, *Bos gaurus*, and the Bison, all of which have strong bony horn-cores, the rugosities of the frontal spread to the orbital and otic region, while in *Bos depressicornis*, in which the horn-cores are weak, the orbital and otic region is smooth. Bearing all these facts in mind, and they could easily be multiplied, and considering furthermore that in Crocodiles the skull bones and the bones of the dermal armour are of altogether different origin but that they nevertheless show the same pattern of sculpture, and that thus also they show the spreading of one feature over the whole body and that something similar occurs in *Lepidosteus* (8), I think it is not too much to assume that also in the primitive *Proavis* the primitive feathers of the tail spread even to regions where they were not wanted. Their attachment on a patagium is the best proof that they never functioned. That the primitive feathers of birds were quills and not, as generally thought, down was recently proved by Steiner (17).

In this way also Beebe's chief argument for the reconstruction of his *Tetrapteryx* loses a great deal of its value. It only shows that first in birds only a marginal row of quills was developed on the arms and on the tail, that later these spread towards the feet, and that the rest of the quills spring up later.

Summing up, one can safely state that in the skeleton of recent

and extinct birds not a single character can be detected which points conclusively towards a primitive arboreal adaptation, but that several skeletal characters can only be explained by the hypothesis of a cursorial running ancestor of birds. The otherwise inexplicable features are: the fused median metatarsals, the reduction of the first metatarsus, the small tarsal bones, the position of the knee, the long symphysis of the pubes in *Archæopteryx*, the lack of clavicles and interclavicle in all birds, and the position of the occipital condyle. The latter is vertical in birds and primitive Dinosaurs, and proves that, unlike arboreal forms, in both these long-necked groups the head was primarily carried upright on a sigmoidal neck.

Apart from all these important points, it is only by means of the running-*Proavis* hypothesis that the early occurrence of numerous flightless birds can be explained. It is evident that badly flying ground birds will much more readily return to exclusively cursorial habits than arboreal birds, for these, before becoming again flightless, must first descend from their trees and become thoroughly adapted to ground life. There exists a great difference between the pelvis of formerly arboreal flightless birds (for example, Dodo) and that of the Palæognathæ.

The hypothesis of a running *Proavis* is also the single one that accounts for the primitive structure of the palate, the free dorsal vertebræ, the low body-temperature, and the strong penis of the greater part of the Palæognathæ, for according to this hypothesis these birds are, of course, much nearer related to *Proavis* than the later and evidently more specialised arboreal birds. If the birds were of arboreal origin, one would expect the most primitive birds among the arboreal and not the terrestrial birds. In compliance with a wish of Steiner (17), I desist from using in the course of these comparisons the term Ratitæ.

That in one primitive arboreal bird more specialised, however, than an ostrich (i. e. *Opisthocomus*) the claws of the wing are more used for climbing than in all the other recent birds, is not of very great weight, for other nestlings use even their beak when climbing, and yet nobody will consider the Parrots to be ancestral to all the other birds. The climbing of *Opisthocomus* may quite well be regarded as a secondary adaptation, for the development of the pinions of the wings in *Opisthocomus* suffers a curious retardation that points in this direction (14). The sternum of *Opisthocomus* shows likewise a curious modification.

The primitive structure of the nest of ground birds when compared with the nest of the arboreal birds, and the more brilliant coloration of the latter, also agree very well with the hypothesis of the terrestrial origin of all birds. Even the curious fact that the nestlings of ground birds as a rule leave their nest comparatively soon after birth seems to some extent to favour this hypothesis (14).

Up to the present all critics of the "running *Proavis*" hypothesis have only tried to find apparent difficulties in that hypothesis,

and have never considered what it explains; now it is their turn to explain all the points that have been brought forward in the course of this paper by means of their hypothesis of an arboreal *Proavis*. It may be that more difficulties will be encountered than are expected.

Some critics (12) say that the comparison of a running *Proavis* with the different flying fishes is no comparison at all, because fishes do not move their pectoral fins in flight. In spite of this, I repeat that the comparison is rather a good one because

- (a) both types are vertebrata in which the anterior limbs are primarily only used for a similar passive gliding;
- (b) in both, during gliding the centre of gravity is behind the upholding surface, giving it a convenient elevation;
- (c) in both types the motive power used on land or in water is situated at the posterior end of the body and behind the gliding-planes;
- (d) in both, the locomotive power can immediately be brought again into action as soon as gliding through the air ceases, and so gliding can soon be regained.

None of these four characters can be found in arboreal passive fliers.

Zschokke (21) has remarked that some Crustacea develop a sort of flying like that of flying fishes; so there is no reason why a terrestrial vertebrate animal should not also have been capable of developing it. No mechanical difficulties exist. To those who go on to argue that, with the exception of flying fishes, all other flying vertebrates descended from arboreal animals, and that therefore this was presumably also the case in birds, I retort that, with the exception of flying snakes, all arboreal vertebrata and naturally all their flying offspring are without exception quadrupedal, while this is not the case in birds.

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EXHIBITIONS AND NOTICES.

March 20th, 1923.

Prof. E. V. MACBRIDE, F.R.S., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of February, 1923:—

The registered additions to the Society's Menagerie during the month of February were 141 in number. Of these 76 were acquired by presentation, 27 were deposited, 17 were purchased, and 21 were born in the Menagerie.

The following may be specially mentioned:—

2 Illiger's Marmosets (*Mystax illigeri*), from the Upper Amazons, new to the Collection, deposited on February 6th.

1 Banded Coati (*Nasua vittata*), from British Guiana, presented by The Viscount Dunsford on February 13th.

4 Reindeer (*Rangifer tarandus*), from Finland, purchased on February 24th.

2 Eared Vultures (*Otogyps auricularis*), from South Africa, purchased on February 16th.

Mr. F. MARTIN DUNCAN, F.R.M.S., F.Z.S., exhibited a specimen of a caterpillar (? *Charagria virescens*) infected with the Entomogenous fungus *Cordyceps robertsii*, which he had recently received from Tauranga, New Zealand. The specimen showed the long stroma of the fungus growing out through the tissues of the joint between the head and first segment of the thorax of the caterpillar, and bearing at its free end the densely packed perithecia; the whole aerial stem bearing a strong resemblance to a miniature bullrush. The native names for this so-called plant-caterpillar are "aweto," "pepeaweto," and "hotete"; and the burnt ashes of these fungus-infested caterpillars, powdered and mixed with water, were used in ceremonial tattooing of rank and tribe.

Mr. M. A. C. HINTON, F.Z.S., exhibited, and made remarks upon, the skin of a Lioness showing considerable development of mane.

April 10th, 1923.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,
in the Chair.

The SECRETARY exhibited, and made remarks upon, a series of photographs of the deep-level reservoirs of the Society's new Aquarium.

Mr. G. C. ROBSON, M.A., F.Z.S., exhibited, and made remarks upon, the snail *Planorbis dufouri* Graells, the intermediate host of *Schistosoma* (*Bilharzia*) *haematobium*, in Portugal.

Dr. G. M. VEYERS, F.Z.S., gave an account of his recent visit to Zoological Gardens in Holland and Belgium.

April 24th, 1923.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of March, 1923 :—

The registered additions to the Society's Menagerie during the month of March were 234 in number. Of these 154 were acquired by presentation, 21 were deposited, 54 were purchased, 1 was received in exchange, and 4 were born in the Menagerie.

The following may be specially mentioned :—

2 Black Spider-Monkeys (*Ateles ater*), from South America, purchased on March 21st.

1 Indian Wild Dog (*Cyon dukhensis*), from the Central Provinces, India, presented by Major T. S. Paterson on March 2nd.

3 Axis Deer (*Axis axis*), from India, presented by James A. de Rothschild, Esq., on March 29th.

1 female Llama, presented by A. H. Wingfield, Esq., F.Z.S., on March 24th.

Capt. R. B. MURRAY, F.G.S., F.R.G.S., exhibited living and mounted specimens of a Giant Centipede from Trinidad, and made the following remarks :—

The two specimens of the Giant Centipede recently presented to the Zoological Gardens were captured on the small island of Gasparee on the west coast of Trinidad and in the Gulf of Paria, which latter separates the island of Trinidad from the Spanish Main, or Venezuela.

The species is confined to the tropical latitudes of South America, and in certain localities is by no means uncommon, as, for instance, amongst the Gulf islands of Trinidad, which enjoy the reputation of breeding "the largest centipedes in the world." Trinidadans are familiar with this little dragon of the islands, yet remarkably enough it is not known to have been found on the mainland of Trinidad, though the whole group of islands are closely associated both geographically and geologically. It is, however, possible that the Gulf islands offer certain peculiar conditions of environment favouring their existence, and that their occurrence on the mainland of Trinidad has escaped observation by reason of their comparative scarcity.

The Giant Centipede is nocturnal in habits, but it may sometimes be found on the move during the day, and when disturbed its rustling passage through the undergrowth is distinctly audible. Occasionally it is found sheltering in the rock fissures leading to a deep-seated Parasol Ants' nest, and when the latter is attacked with a chemical exterminator the bewildered lodger emerges.

Lieut.-Col. S. MONCKTON COPEMAN, M.D., F.R.S., and Major E. E. AUSTEN, D.S.O., F.Z.S., exhibited, and made remarks upon, photographs and specimens of the rare fly *Hylephilas obtusa* Zett. The exhibition included the only male of this species captured in this country in the neighbourhood of the burrows of the bee *Andrena fulva*, on which the female of this fly is parasitic. The specimen was captured on Primrose Hill, London.

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ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

February 6th, 1923.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the months of November and December 1922.

LORD ROTHSCHILD, F.R.S., F.Z.S., exhibited an adult male *Gorilla gorilla beringeri* from near Lake Kivu, and further illustrated his remarks by a series of lantern-slides.

MR. OLDFIELD THOMAS, F.R.S., F.Z.S., exhibited a new Rock-Kangaroo, which he diagnosed as follows :

Petrogale godmani, sp. n.

Like *P. assimilis*, but with a whitish tail, broader nasals, and larger secator.

Hab. Black Mountain, near Cooktown, N. Queensland.

Type. B.M. No. 23.1.5.19. Presented by the Trustees of the Godman Exploration Fund.

Mr. Thomas explained to the Meeting about the Godman Exploration Trust, which had been founded in memory of her husband by Dame Alice Godman, and from which it was hoped much benefit would be gained by the Museum.

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. THOMAS also exhibited the skull of a Pygmy Fruit-Bat from Sumatra, upon which he had founded a new genus. He proposed to substitute *Ethalops* for the preoccupied name *Ethalodes*, which he had inadvertently given to the new genus of Fruit Bats described in the 'Annals and Magazine of Natural History' for February.

Mr. J. B. SCRIVENOR, M.A., exhibited, and made remarks upon, a photograph showing the method adopted by Malay natives in breaking in recently captured Elephants.

Mr. C. A. ADAIR DIGHTON, M.B., F.R.C.S., F.Z.S., gave a *résumé* of his paper on "Coat-colour in Greyhounds."

Mr. E. G. BOULENGER, F.Z.S., gave an account of his recent visit to Vienna and of the experiments carried on there by Dr. Kammerer and others upon Amphibians and Insects.

In the absence of the Author, Professor WATSON, F.R.S., F.Z.S., gave an account of a paper by Mr. E. LEONARD GILL, M.Sc., entitled "The Permian Fishes of the Genus *Acentrophorus*."

The following communications were taken as read:—CHARLES F. SONNTAG, M.D., F.Z.S., "On the Vagus and Sympathetic Nerves of the Terrestrial Carnivora"; EDWARD PHELPS ALLIS, JR., F.R.M.S., F.Z.S., "The Postorbital Articulation of the Palato-quadrate with the Neurocranium in the Cœlacanthidæ"; GEORGE S. GIGLIOLI, M.D., "On the Linguatulid Arachnid, *Railietiella furcocerca* (Diesing, 1835), Sambon, 1922"; The late Mrs. RITA MARKBREITER, B.Sc., "Some *Microfilaria* found in the Blood of Birds dying in the Zoological Gardens, 1920-1922."

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 20th, 1923, at 5.30 p.m., when the following Communications will be made:—

THE SECRETARY.

Report on the Additions to the Society's Menagerie during the month of January 1923.

Prof. H. M. LEFROY, F.Z.S.

Exhibition of a Cinematograph film of the House-fly.

Dr. N. S. LUCAS, F.Z.S.

Reports on the Deaths which have occurred in the Society's Gardens during 1922.

Prof. EINAR LÖNNBERG, F.M.Z.S.

Remarks on some Palearctic Bears.

E. W. SHANN, B.Sc., F.Z.S.

The Embryonic Development of the Porbeagle-Shark, *Lamna cornubica*.

ROBERT GURNEY, M.A., F.Z.S.

Some Notes on *Leander longirostris*, M.-Edwards, and other British Prawns.

The following Papers have been received:—

CHAS. F. SONNTAG, M.D., F.Z.S.

The Comparative Anatomy of Tongues of the Mammalia.—VIII. Carnivora.

R. KIRKPATRICK, F.Z.S.

On a new Species of the Tunicate *Rhizomolgula* with remarkable Sensory Organs. No. 24. Results of the Oxford University Expedition to Spitzbergen. 1921.

T. H. RING.

The Elephant-Seals of Kerguelen Land.

SUSHIL CH. SARKAR, F.Z.S.

A Comparative Study of the Buccal Glands and Teeth of the Opisthoglypha, and a Discussion on the Evolution of the Order from Aglypha

H. G. CANNON, B.A., F.Z.S.

A Note on the Zœa of a Land-Crab, *Cardisoma armatum*.

JOSEPH CONRAD CHAMBERLIN.

A Systematic Monograph of the Tachardiinæ or Lac Insects (Hemiptera--Coccidæ).

OLDFIELD THOMAS, F.R.S., F.Z.S., and M. A. C. HINTON.

On the Mammals obtained in Darfur by the Lynes-Lowe Expedition.

R. I. Pocock, F.R.S., F.Z.S.

(1) On the External Characters of *Elaphurus*, *Hydropotes*, *Pudu*, and other Cervidæ.

(2) The Classification of the Sciuridæ.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.

February 13th, 1923.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

February 20th, 1923.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of January 1923.

Mr. D. SETH SMITH, F.Z.S., exhibited a number of skins of Birds-of-Paradise and gave an account of the various forms of sexual display, drawing special attention to the display of the Magnificent Bird-of-Paradise (*Diphyllodes magnifica hunsteini*), a living specimen being now in the Society's collection of tropical birds.

A Cinematograph record of the life-history of the House-fly, taken under the direction of Prof. H. M. LEFROY, F.Z.S., was exhibited.

The SECRETARY exhibited a photograph of the Polar Bears "Sam and Barbara."

Mr. R. I. POCKOCK, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of drawings of the feet and nose of the Polar Bear.

Dr. N. S. LUCAS, F.Z.S., communicated his Report on the Deaths which occurred in the Society's Gardens during 1922.

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The following papers were taken as read :—Prof. EINAR LÖNNBERG, F.M.Z.S., “Remarks on some Palearctic Bears”; E. W. SHANN, B.Sc., F.Z.S., “The Embryonic Development of the Porbeagle-Shark, *Lamna cornubica*”; ROBERT GURNEY, M.A., F.Z.S., “Some Notes on *Leander longirostris*, M.-Edwards, and other British Prawns.”

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 6th, 1923, at 5.30 p.m., when the following communications will be made :—

H. G. CANNON, B.A., F.Z.S.

A Note on the Zœa of the Land-Crab, *Cardisoma armatum*.

MISS L. E. CHEESMAN, F.E.S., F.Z.S.

Notes on the Pairing of the Land-Crab, *Cardisoma armatum*.

CHAS. F. SONNTAG, M.D., F.Z.S.

The Comparative Anatomy of Tongues of the Mammalia.—
VIII. Carnivora.

R. KIRKPATRICK, F.Z.S.

On a new Species of the Tunicate *Rhizomolgula* with remarkable Sensory Organs. No. 24. Results of the Oxford University Expedition to Spitzbergen, 1921.

T. H. RING.

The Elephant-Seals of Kerguelen Island.

The following Papers have been received :—

SUSHIL CH. SARKAR, F.Z.S.

A Comparative Study of the Buccal Glands and Teeth of Opisthoglyph Snakes, and a Discussion on the Evolution of the Order from Aglypha.

OLDFIELD THOMAS, F.R.S., F.Z.S., and M. A. C. HINTON, F.Z.S.

On the Mammals obtained in Darfur by the Lynes-Lowe Expedition.

R. I. Pocock, F.R.S., F.Z.S.

(1) On the External Characters of *Elaphurus*, *Hydropotes*, *Pudu*, and other Cervidæ.

(2) The Classification of the Sciuridæ.

JOSEPH CONRAD CHAMBERLIN.

A Systematic Monograph of the Tachardiinæ or Lac Insects (Hemiptera—Coccidæ).

Prof. K. KOSTANECKI, M.D., LL.D.

On a Remnant of the Omphalo-mesenteric Arteries in the Manatee.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

February 27th, 1923.

No. 237.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

March 6th, 1923.

Sir S. F. HARMER, K.B.E., F.R.S., Vice-President,
in the Chair.

The SECRETARY read a note from Mr. CALDWELL of the Game Warden's Office, Nairobi, on a case of apparent melanism in Tippelskirch's Giraffe (*Giraffa camelopardalis tippelskirchi*).

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of drawings of the feet and spurs of the Echidna.

In the absence of Sir G. ABERCROMBY, Mr. R. I. Pocock exhibited the mounted head of a Kob from East Africa.

Prof. E. W. MacBride, F.R.S., F.Z.S., exhibited, and made remarks upon, a series of photomicrographs of sections through the nuptial callosities of Frogs of the genera *Rana* and *Alytes*.

Mr. F. M. Swynnerton, C.M.Z.S., exhibited, and made remarks upon, the stomach-contents of a Crocodile.

Mr. H. G. Cannon, B.A., F.Z.S., communicated his paper "A Note on the Zœa of the Land-Crab, *Cardisoma armatum*."

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Miss L. E. CHEESMAN, F.E.S., F.Z.S., communicated her paper "Notes on the Pairing of the Land-Crab, *Cardisoma armatum*."

Dr. CHAS. F. SONNTAG, F.Z.S., gave a *résumé* of his paper on "The Comparative Anatomy of the Tongues of the Mammalia.—VIII. Carnivora."

Mr. W. P. PYCRAFT, F.Z.S., gave a *résumé* of Mr. T. H. RING's paper on "The Elephant-Seals of Kerguelen Land."

Mr. R. KIRKPATRICK, F.Z.S., communicated his paper "On the Tunicate *Rhizomolgula globularis* Pallas. No. 24. Results of the Oxford University Expedition to Spitzbergen, 1921" *.

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 20th, 1923, at 5.30 P.M., when the following communications will be made:—

SUSHIL CH. SARKAR, F.Z.S.

A Comparative Study of the Buccal Glands and Teeth of Opisthoglyph Snakes, and a Discussion on the Evolution of the Order from Aglypha.

OLDFIELD THOMAS, F.R.S., F.Z.S., and M. A. C. HINTON, F.Z.S.

On the Mammals obtained in Darfur by the Lynes-Lowe Expedition.

R. I. POCCOCK, F.R.S., F.Z.S.

- (1) On the External Characters of *Elaphurus*, *Hydropotes*, *Pudu*, and other Cervidæ.
- (2) The Classification of the Sciuridæ.

* [Title changed from that announced in Abstract No. 236.—EDITOR.]

The following Papers have been received:—

JOSEPH CONRAD CHAMBERLIN.

A Systematic Monograph of the Tachardiinæ or Lac Insects
(Hemiptera—Coccidæ).

Prof. K. KOSTANECKI, M.D., LL.D.

On a Remnant of the Omphalo-mesenteric Arteries in the
Manatee.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited as far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

March 13th, 1923.

No. 238.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

March 20th, 1923.

Prof. E. W. MacBRIDE, F.R.S., Vice-President,
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of February 1923.

Mr. F. MARTIN DUNCAN, F.R.M.S., F.Z.S., exhibited, and made remarks upon, a specimen and photographs of a Caterpillar from New Zealand infected with the Entomogenous fungus *Cordyceps robertii* Hooker.

Mr. M. A. C. HINTON, F.Z.S., exhibited, and made remarks upon, the skin of a Lioness.

Dr. PHILIPPA C. ESDAILE, F.Z.S., gave a *résumé* of Mr. SUSHIL CH. SARKAR's paper on "A Comparative Study of the Buccal Glands and Teeth of Opisthoglyph Snakes, and a Discussion on the Evolution of the Order from Aglypha."

A paper "On the Mammals obtained in Darfur by the Lynes-Lowe Expedition" by Mr. OLDFIELD THOMAS, F.R.S., F.Z.S., and Mr. M. A. C. HINTON, F.Z.S., was communicated by Mr. HINTON.

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Mr. R. I. Pocock, F.R.S., F.Z.S., gave a *résumé* of his papers
 “(1) On the External Characters of *Elaphus*, *Hydropotes*, *Pudu*,
 and other Cervidæ” and “(2) The Classification of the Sciuridæ.”

The next Meeting of the Society for Scientific Business will be
 held on Tuesday, April 10th, 1923, at 5.30 p.m., when the
 following communications will be made:—

Dr. G. M. VEVERS, F.Z.S.

Notes on a recent visit to Zoological Gardens in Holland
 and Belgium.

Prof. K. KOSTANECKI, M.D., LL.D.

On a Remnant of the Omphalo-mesenteric Arteries in the
 Manatee.

Dr. CHAS. F. SONNTAG, F.Z.S.

On the Anatomy, Physiology, and Pathology of the Chim-
 panzee.

The following Paper has been received:—

E. C. STUART BAKER, F.Z.S.

Cuckoos' Eggs and Evolution.

The Publication Committee desire to call the attention of
 those who propose to offer Papers to the Society, to the great
 increase in the cost of paper and printing. This will render it
 necessary for the present that papers should be condensed, and
 be limited so far as possible to the description of new results.

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Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
March 27th, 1923.

No. 239.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

April 10th, 1923.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,
in the Chair.

THE SECRETARY exhibited, and made remarks upon, a series of photographs of the deep-level reservoirs of the Society's new Aquarium.

Mr. G. C. ROBSON, M.A., F.Z.S., exhibited, and made remarks upon, the snail *Planorbis sufouri* Graells, the intermediate host of *Schistosoma (Bilharzia) hæmatobium*, in Portugal.

Dr. G. M. VEVERS, F.Z.S., gave an account of his recent visit to Zoological Gardens in Holland and Belgium.

Dr. CHAS. F. SONNTAG, F.Z.S., gave a *résumé* of his paper "On the Anatomy, Physiology, and Pathology of the Chimpanzee."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum. payable in advance.

In the absence of the Author, Prof. K. Kostanecki's paper "On a Remnant of the Omphalo-mesenteric Arteries in the Manatee," was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, April 24th, 1923, at 5.30 P.M., when the following communications will be made:—

R. B. MURRAY, F.G.S., F.R.G.S.

Exhibition of a Giant Centipede from Trinidad, and mounted skins of Oil-birds.

Lt.-Col. S. MONCKTON COPEMAN, M.D., F.R.S., and Major E. E. AUSTEN, D.S.O., F.R.S.

Exhibition (with photographs) of an unique British Dipteran, taken on Primrose Hill.

Baron F. NOPCSA.

On the origin of flight in Birds.

E. C. STUART BAKER, F.Z.S.

Cuckoos' Eggs and Evolution.

The following Paper has been received:—

HARRY BURRELL, C.M.Z.S.

The Transmission of Marsupial Embryos.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited as far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
April 17th, 1923.

No. 240.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

April 24th, 1923.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of March 1923.

Capt. R. B. MURRAY, F.G.S., F.R.G.S., exhibited, and made remarks upon, mounted and living specimens of a giant Centipede from Trinidad.

Lt.-Col. S. MONCKTON COPEMAN, M.D., F.R.S., F.Z.S., and Major E. E. AUSTEN, D.S.O., F.Z.S., exhibited, and made remarks upon, photographs and specimens of an unique British Dipteron, taken on Primrose Hill.

Baron F. NOPCSA gave a *résumé* of his paper "On the Origin of Flight in Birds."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. E. C. STUART BAKER, F.Z.S., communicated his paper on
 "Cuckoos' Eggs and Evolution."

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 8th, at 5.30 P.M., when the following communications will be made:—

THE SECRETARY.

Exhibition of Photographs of Big Game from Choma,
 Northern Rhodesia.

Miss L. E. CHEESMAN, F.E.S., F.Z.S.

(1) Exhibition of living specimens of *Peripatus* from
 Trinidad.

(2) Exhibition of section of a nest of the Stingless Bee
 from Australia.

HARRY BURRELL, C.M.Z.S.

Note on a hibernating female specimen of the Marsupial
Acrobates pygmaeus.

F. MARTIN DUNCAN, F.R.M.S., F.Z.S.

On the Microscopic Structure of Mammalian Hairs.—I. The
 Hairs of the Primates.

The following Paper has been received:—

C. TATE REGAN, M.A., F.R.S., F.Z.S.

The Skeleton of *Lepidosteus*, with Remarks on the Origin
 and Evolution of the Lower Neopterygian Fishes.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

May 1st, 1923.

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